

## The Structure, Development, and Bionomics of the House-fly, *Musca domestica*, Linn.

Part III.—The Bionomics, Allies, Parasites, and the Relations  
of *M. domestica* to Human Disease.

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With Plate 22.

### CONTENTS.

	PAGE
I. Introduction . . . . .	348
II. Distribution . . . . .	349
III. Flies occurring as Co-inhabitants of Houses with <i>M. domestica</i> or as Visitants . . . . .	351
IV. Physiology :	
1. Influence of Food, Temperature, and Light . . . . .	362
2. Hibernation . . . . .	363
3. Flight . . . . .	364
4. Regeneration of Lost Parts . . . . .	365
V. Natural Enemies and Occasional Parasites :	
1. <i>Chernes nodosus</i> , Schrank . . . . .	367
2. Acarina or Mites borne by House-flies . . . . .	369
3. Fungal parasite— <i>Empusa muscæ</i> , Cohn . . . . .	371
VI. True Parasites :	
1. Flagellata— <i>Herpetomonas muscæ-domesticæ</i> . . . . .	374
<i>Crithidia muscæ-domesticæ</i> . . . . .	379
2. Nematoda— <i>Habronema muscæ</i> . . . . .	380
3. Dissemination of Parasitic Worms . . . . .	382
VII. Dissemination of Pathogenic Organisms by <i>M. domestica</i> and its non-Blood-sucking Allies :	
1. Typhoid Fever . . . . .	385
2. Anthrax . . . . .	394
3. Cholera . . . . .	396
4. Tuberculosis . . . . .	398

	PAGE
5. Ophthalmia . . . . .	399
6. Plague . . . . .	401
7. Miscellanea . . . . .	402
VIII. Flies and Intestinal Myiasis . . . . .	404
IX. Literature . . . . .	405
X. Appendix on the Winter Breeding of <i>M. domestica</i> . . . . .	412

## I. INTRODUCTION.

THE present paper concludes this study of the structure, development, and bionomics of *Musca domestica* (the previous parts were published in 1907 and 1908). In it I have described the bionomics, certain of its allies which may occur in houses, its parasites, and its relation to man, especially as the carrier of the bacilli of certain infectious diseases.

The last portion of the present paper, in which is described what is known concerning the ability of *M. domestica* and its allies to carry and disseminate the bacteria of many important diseases, shows, I hope, the grave character of its relation to man. Although its importance in this respect is being gradually realised in this country, it is not so widely recognised as it should be. In the United States of America it is proposed to change this insect's name from the house-fly to the "Typhoid fly"; notwithstanding certain objections to this name, it clearly indicates that more attention must be paid to preventive measures, that is, they must be reduced by the deprivation of suitable breeding-places. I have not discussed in the present paper the relation of house-flies to infantile or summer diarrhœa, chiefly because we are not yet certain as to the specific cause, but this disease may be included for the present under typhoid or enteric fever in so far as the relation of flies with it is concerned.

I should like to take this opportunity of thanking those medical men, whose names I mention later, for the kind manner in which they have replied to my inquiries concerning their observations on various diseases of which they have special knowledge.

## II. DISTRIBUTION.

*Musca domestica* is probably the most widely distributed insect to be found; the animal most commonly associated with man, whom it appears to have followed over the entire globe. It extends from the sub-polar regions, where Linnæus refers to its occurrence in Lapland, and Finmark as "rara avis in Lapponia, at in Finmarchia Norwegiæ integras domos fere replet," to the tropics, where it occurs in enormous numbers. Referring to its abundance in a house near Pará in equatorial Brazil, Austen (1904) says: "At the mid-day meal they swarmed on the table in almost inconceivable numbers," and other travellers in different tropical countries have related similar experiences to me, how they swarm round each piece of food as it is carried to the mouth.

In the civilised and populated regions of the world it occurs commonly, and the British Museum (Natural History) collection and my own contain specimens from the following localities. Certain of the localities have, in addition, been obtained from lists of insect faunas:

Asia.—Aden; North West Provinces (India); Calcutta; Madras; Bombay (it probably occurs over the whole of India); Ceylon; Central China; Hong-Kong; Shanghai; Straits Settlements; Japan.

Africa.—Port Said; Suez; Egypt; Somaliland; Nyassaland; Uganda; British E. Africa; Rhodesia; Transvaal; Natal; Cape Colony; Madagascar; Northern and Southern Nigeria; St. Helena; Madeira.

America.—Distributed over North America; Brazil; Monte Video (Uruguay); Argentine; Valparaiso; West Indies.

Australia and New Zealand.

Europe and the isles of the Mediterranean; it is especially common in Cyprus.

Not only is this world-wide distribution of interest, but its distribution in our own country is noteworthy. From observations that I have made during a number of years in town and

suburban houses and country houses and cottages, I find that in the former it is by far the commonest house-fly. But whereas *M. domestica* may be almost the only species in warm places where food is present, such as restaurants and kitchens, in other rooms of houses *Homalomyia canicularis*, the small house-fly, increases in proportion and often predominates; occasionally one may find it to be commoner than *M. domestica*. In country houses the proportions vary by the intrusion of *Stomoxys calcitrans*, which I have often found to be the dominant species. In a certain country cottage, out of the several hundreds captured, *S. calcitrans* formed 50 per cent. of the total, the rest being chiefly *H. canicularis* together with *Anthomyia radicum*, whose larvæ, as I have shown (1907), breed in horse-manure with those of *M. domestica*. The following records taken from a "fly census" that was made in 1907 may be taken as illustrative of the proportional abundance of the different species in different situations; although the numbers of these records are small the proportions are more obvious.

Place.	<i>M. domestica</i> .	<i>H. canicularis</i> .	Other species.
Restaurant, Manchester .	1869	14	2 ( <i>M. stabulans</i> , <i>C. erythrocephala</i> ).
Kitchen, detached suburban house (six records), Lancashire . . . . .	581	265	14
Kitchen, detached suburban house in Manchester	682	7	14
Stable, suburban house .	22	153	14 (12. <i>S. calcitrans</i> ).
Bedroom, suburban house .	1	33	4 ( <i>M. stabulans</i> ).

Out of a total of 3856 flies caught in different situations, such as restaurants, kitchens, stables, bedrooms and hotels, 87.5 per cent. were *M. domestica*, 11.5 per cent. *H. canicularis*, and the rest were other species such as *S. calcitrans*, *Muscina stabulans*, *C. erythrocephala*, and *Anthomyia radicum*. These figures are comparatively small, but



are representative of the average occurrence, as I have observed, of the different species.

For the proportional occurrence in similar localities we have interesting figures given by Howard (1900) for the United States. Of 23,087 flies caught in rooms where food supplies are exposed he found that 22,808, or 98·8 per cent. of the whole number, were *M. domestica*, and of the remaining 1·2 per cent. *H. canicularis* was the commonest species. Hamer (1908) found that more than nine tenths of the flies caught in the kitchens and "living-rooms" of houses in the neighbourhood of depôts for horse-refuse, manure, etc., were *M. domestica*. In a further report Hamer gives more details as to the different species that were found. In one lot of 35,000 flies caught on four fly-papers exposed in similar positions, 17 per cent. were *Homalomyia canicularis*, less than 1 per cent. were *C. erythrocephala*, and considerably less than 1 per cent. were *Muscina stabulans*, whereas of nearly 6000 flies caught in another situation in four fly-balloons 24 per cent. were *H. canicularis*, 15 per cent. were *C. erythrocephala*, and nearly 2 per cent. were *M. stabulans*. He gives an interesting diagram showing from counts of flies the seasonal prevalence which I have previously recorded from observation. The report shows how the proportions of the different species vary in different situations according to the substances and refuse that are present in the locality. We may therefore say with certainty that *M. domestica* is the commonest species of house-fly, and next to this *H. canicularis*, and that in country houses *S. calcitrans* often occurs in large numbers, although it is not a house-fly in the strict sense of the word.

### III. FLIES OCCURRING AS CO-INHABITANTS OF HOUSES WITH *M. DOMESTICA* OR AS VISITANTS.

We have seen from the preceding section that *M. domestica* is by far the commonest species which occurs in houses, and is, in fact, "domesticated" in the true sense of the word

—Linnaeus never selected a more truly specific title; nevertheless, other species of closely allied flies are found in houses. These may be either co-inhabitants, that is, living in houses, as in the case of *H. canicularis* and one or two others to be mentioned subsequently, or they may be visitants. The visitants normally lead an open-air life, but sometimes, as in the case of *Stomoxys calcitrans*, they spend a portion of their time in houses, when climatic conditions are less favourable for out-door life. Such flies as the blow-fly, or "blue-bottle," *Calliphora erythrocephala*, and its allies, enter houses only in search of suitable substances upon which to deposit their eggs. The appearance in houses of certain flies, as, for example, *Pollenia rudis*, can only be regarded as accidental, and the cause may be often traced to the occurrence of climbing plants such as ivy or other creepers on the walls of the house.

In India two species of flies closely allied to *M. domestica* are found—*Musca domestica* sub-sp. *determinata* Walker and *M. enteniata*, both of which, on account of their close resemblance to *M. domestica* and the similarity of their breeding habits, are frequently mistaken for it.

(1) *M. domestica* sub-sp. *determinata* Walker.

This Indian variety of the house-fly was described by Walker (1856) from the East Indies. His description is as follows: "Black, with a hoary covering; head with a white covering; frontalia broad, black, narrower towards the feelers; eyes bare; palpi and feelers black; chest with four black stripes; abdomen cinereous, with a large tawny spot on each side at the base; legs black; wings slightly grey, with a tawny tinge at the base; præbrachial vein forming a very obtuse angle at its flexure, very slightly bent inward from thence to the tip; lower cross-vein almost straight; alulæ whitish, with pale yellow borders; halteres tawny."

In appearance and size it is very similar to *M. domestica*. Its breeding habits are also similar. Aldridge (1904) states

that at certain seasons of the year it is present in enormous numbers. The method of disposal of the night soil is to bury it in trenches about one foot or less in depth. From one sixth of a cubic foot of soil taken from a trench at Meerut and placed in a cage, 4042 flies were hatched. Lieut. Dwyer collected 500 from one cage covering three square feet of a trench at Mhow. Specimens in the British Museum collection were obtained from the hospital kitchens, and Smith found them in a ward at Benares.

They have also been recorded from the N.W. Provinces, Kangra Valley (4500 feet), Dersa, and I have received specimens from Aden.

(2) *Musca enteniata* Bigot.

This fly has a distribution somewhat similar to the last species, and like it, has a marked resemblance to *M. domestica*, as Bigot's (1887) description indicates :

“ Front très étroit, les yeux, toutefois, séparés. Antennes et palpes noirs ; face et joues blanches ; thorax noir avec trois larges bandes longitudinales grises ; flancs grisâtres, écusson noir avec deux bandes semblables ; cuillerons et balanciers d'un jaunâtre très pâle ; abdomen fauve, avec une bande dorsale noir et quelques reflets blancs ; pieds noirs ; ailes hyalines ; cinquième nervure longitudinal (Rondin) coudée suivant un angle légèrement arrondi, ensuite un peu concave ; deuxième transversale (l'extrême) presque perpendiculaire, légèrement bisinueuse, soudée à la cinquième longitudinale, à égale distance du conde et de la première nervure transversale (l'interne).”

*M. enteniata* measures 4 to 5 mm. in length. The British Museum collection contains specimens sent by Major F. Smith from Benares, with these notes : “ Bred from human ordure ; hospital ward fly ; at an enteric stool ; bred from cow-dung fuel cakes.” I have received specimens from Suez and Aden, and it is recorded as breeding in human excrement in Khartoum (Balfour, 1908) and in stable refuse, as also M

*domestica* and *M. corvina*. It will be seen, therefore, that its breeding habits are very similar to those of *M. domestica* and the sub-species *determinata*. It is interesting and important to note the rather exceptional choice of cow-dung as a breeding-place.

(3) *Homalomyia canicularis* L.

This species of fly (see 'Quart. Journ. Micr. Sci.,' vol. 51, Pl. 22, fig. 3) is often mistaken by the uninitiated for *M. domestica* which are not full grown. Although it may be called the small or lesser house-fly its differences from *M. domestica* are great, as it belongs to a different group of calypterate Muscidae, namely, the Anthomyiidae. One of the chief distinguishing features of this group is that the fourth longitudinal vein of the wing (*M.* 1 + 2) goes straight to the margin of the wing and does not bend upwards at an angle as in *M. domestica*.

The male of *H. canicularis* differs from the female in some respects. In the male the eyes are close together, and the frontal region is consequently very narrow; the sides of this, these are the inner orbital regions, are silvery white, separated by a narrow black frontal stripe. In the female the space between the inner margins of the eyes is about one third of the width of the head; the frons is brownish black, and the inner orbital regions are dark ashy grey. The bristle of the antenna of *H. canicularis* is bare; in *M. domestica*, it will be remembered, the bristle bears a row of setae on its upper and lower sides. The dorsal side of the thorax of the male is blackish grey with three rather indistinct longitudinal black lines. In the female it is of a lighter grey, and the three longitudinal stripes are consequently more distinct. The abdomen of the male *H. canicularis* is narrow and tapering compared with that of *M. domestica*. It is bronze black in colour, and each of the three abdominal segments has a lateral translucent area, so that when it is seen against the light, as on a window-pane, three, and sometimes four, pairs of yellow translucent areas can be seen by the trans-

mitted light. In the female the abdomen is short in proportion to its length, and is of a greenish or brownish-grey colour.

*H. canicularis* appears in houses before *M. domestica*, and can be found generally in May and June. In the latter month its numbers are swamped, as it were, by *M. domestica*, and it appears to seek the other rooms of a house than the kitchen, although I have found it frequently in considerable numbers in kitchens. The average length is 5.7 mm.

The larva of *H. canicularis* (Pl. 22, fig. 1) is very distinct from that of *M. domestica*, as will be seen from the figure. It is compressed dorso-ventrally, and has a double row of processes on each side. Owing to the rough and spinous nature of these processes dirt adheres to the larva and gives it a dirty-brown appearance. The full-grown larva measures 5-6 mm. in length. The breeding habits of *H. canicularis* are very similar to those of *M. domestica*. The larvæ feed on waste vegetable substances and also on various excremental products, but particularly, I have found, on human excrement, for which they show a great partiality. I have frequently found excrement in privy middens to be a moving mass of the larvæ of *H. canicularis*. The larval period is from three to four weeks, and the insect spends fourteen to twenty-one days in the pupal stage.

#### (4) *Homalomyia scalaris* F.

Newstead (1907) has found this species occurring as a house-fly. It is slightly larger than, though similar in many respects to, *H. canicularis*. The larva is very similar in appearance. Newstead found the larvæ in ash-pit refuse, and bred the flies from human fæces. The larvæ have been found frequently to be the cause of intestinal myiasis.

#### (5) *Anthomyia radicum* Meigen.

This member of the Anthomyidæ has been found in houses, especially those in or near the country. The female has been illustrated already (Part I, 'Quart. Journ. Micr. Sci.,' vol. 51, Pl. 22, fig. 2). The male is darker in colour, the dorsal side

of the thorax being blackish with three black longitudinal stripes; the frontal region is very narrow; the abdomen is grey with a dark median stripe. The average length of the body is 5 mm.

In the summer they are common and may be found in the neighbourhood of manure. The eggs are laid in this substance, especially in horse-manure. The larvæ have also been found feeding on the roots of various cultivated cruciferous plants, from which the insect has derived the name "root-maggot." The eggs hatch out from eighteen to thirty-six hours after deposition. The first larval stadium lasts twenty-four hours, the second forty-eight hours, and five days later the larva changes into a pupa, the whole larval life occupying about eight days. The pupal stage lasts ten days, so that in warm weather the development may be completed in nineteen to twenty days. The full-grown larvæ measure 8 mm. in length, and may be distinguished by the tubercles surrounding the caudal extremity. In this species there are six pairs of spinous tubercles surrounding the posterior end and a seventh pair is situated on the ventral surface posterior to the anus. The tubercles of the sixth pair, counting from the dorsal side, are smaller than the rest and are bifid. The arrangement of the tubercles can be seen in fig. 2. The anterior spiracular processes (fig. 3) are yellow in colour and have thirteen lobes.

#### (6) *Stomoxys calcitrans* Linn.

The species is common, especially in the country from July to October, and during these months it may be often found in houses, although Hamer's observations (1908) appear to indicate that the presence of cowsheds, in which they occur in large numbers, does not affect their numbers in houses. I have found *S. calcitrans* in large numbers in the windows of a country house in March and April, and it may be found frequently out of doors on a sunny day in May, and throughout the ensuing summer months. It is normally an outdoor insect, but appears to seek the shelter



of houses, especially during wet weather, from which habit it has no doubt derived the popular name of "storm-fly"; it is also known as the "stable-fly." As these names may be equally applicable to certain other Diptera they should be discarded.

As I have already mentioned this species is frequently mistaken by the public for *M. domestica*, which is supposed to have adopted the biting habit, although the latter is unable to inflict the slightest prick. If examined side by side the great differences between the two will be seen readily (see Part I in 'Quart. Journ. Micr. Sci., vol. 51, Pl. 22, fig. 4). *S. calcitrans* has an awl-like proboscis for piercing and blood-sucking; this projects horizontally forward from beneath the surface of the head (fig. 4). It is slightly larger and more robust than *M. domestica*; the bristles of the antennæ bear setæ on their upper sides only. The colour is brownish with a greenish tinge; the dorsal side of the thorax has four dark longitudinal stripes, the outermost pair being interrupted. At the anterior end of the dorsal side of the thorax the medium light-coloured stripe has a golden appearance, which is very distinct when the insect is seen against the light. The abdomen is broad in proportion to its length, and each of the large second and third segments has a single median and two lateral brown spots; there is also a median spot on the fourth segment.

The life-history of *S. calcitrans* has been studied by Newstead (1906), and I have been able to confirm his observations during 1907 and 1908. From fifty to seventy eggs, measuring 1 mm. in length, are laid by the female. The eggs are laid on warm, decaying vegetable refuse, especially in heaps of fermenting grass cut from lawns; I have frequently confirmed this observation of Newstead's. The eggs are also deposited on various excremental substances upon which the larvæ feed. Osborne (1896) reared them in horse-manure; Howard (1900) states that they live in fresh horse-manure, and records their occurrence in outdoor privies in some localities; Newstead reared them in moist sheep's dung; they can also be reared in cow-dung.



The larvæ are creamy-white in colour and have a shiny, translucent appearance. They are rather similar to those of *M. domestica*, but can be distinguished by the character of the posterior spiracles. These (fig. 5 and 6) are wider apart than in *M. domestica* and are triangular in shape with rounded corners; each of the corners subtends a space in which a sinuous aperture lies. The centre of the spiracle is occupied by a circular plate of chitin. The anterior spiracular processes are five-lobed. Under warm conditions Newstead found that the egg state lasted from two to three days; the larval stage lasts from fourteen to twenty-one days and the pupal stage nine to thirteen days. There are three larval stages. The whole life-history may be complete in twenty-five to thirty-seven days. Some specimens passed the winter in the pupal state.

Although *S. calcitrans* does not frequent to such a great extent as *M. domestica* material likely to contain pathogenic intestinal bacilli, on account of its blood-sucking habits, which cause it to attack cattle and not infrequently man, it may occasionally transfer the anthrax bacillus, as many have believed, and give rise to malignant pustule, etc.

#### (7) *Calliphora erythrocephala* Mg.

This is the commoner of the two English blow-flies or "blue-bottles." The other species, *Calliphora (Musca) vomitoria*, is less common, although the name is frequently given to both species indiscriminately. They can be distinguished, however, by the fact that in *C. erythrocephala* the genæ are fulvous to golden-yellow and are beset with black hairs, whereas in *C. vomitoria* the genæ are black and the hairs are golden-red.

The appearance of *C. erythrocephala* is sufficiently well known with its bluish-black thorax and dark metallic blue abdomen. Its length varies from 7 to 13 mm. The larvæ are necrophagous. The flies deposit their eggs on any fresh or decaying meat, nor is such flesh always dead. On one occasion, when obtaining fresh material in the form of wild

rabbits upon which to rear the larvæ of *C. erythrocephala*, I found the broken leg of a live rabbit, which had been caught in a spring trap set the previous evening, a living mass of small larvæ, which were devouring the animal while it was still alive. An enormous number of eggs are laid by a single insect; Portchinski ('Osten. Sacken,' 1887) found from 450 to 600 eggs, though I have not found so many. With an average mean temperature of 23° C. (73·5° F.) and using fresh rabbits as food for the larvæ, the following were the shortest times in which I reared *C. erythrocephala*. The eggs hatched from ten to twenty hours after deposition. The larvæ underwent the first ecdysis eighteen to twenty-four hours after hatching; the second moult took place twenty-four hours later, and the third larval stage lasted six days, the whole larva life being passed in seven and a half to eight days. Fourteen days were spent in the pupal state; thus the development was complete in twenty-two to twenty-three days. I have no doubt that this time could be shortened by the presence of a very plentiful supply of food, as an enormous amount, comparatively, is consumed.

The full-grown larva may measure as much as 18 mm. in length. The posterior extremity is surrounded by six pairs of tubercles arranged as shown in the figure (fig. 12); there is also a pair of anal tubercles. The anterior spiracular (fig. 11) processes are nine-lobed. The posterior spiracles (fig. 10) are circular in shape and contain three slit-like apertures. In the second larval instar (fig. 9) there are only two slits in each of the posterior spiracles, and in the first larval instar (fig. 8) each of the posterior spiracles consists of a pair of small slit-like orifices. Howard (1900) found the fly on fresh human fæces, and Riley records it as destroying the Rocky Mountain locust.

*C. erythrocephala* is an outdoor fly, but frequently enters houses in search of material upon which to deposit its eggs and also for shelter. From its habit of frequenting fæces, which may be observed in this country especially in insanitary court-yards, and such food as meat and fruit, it is not improb-

able that it occasionally may bear intestinal bacilli on its appendages or body and thus carry infection. Its flesh-seeking habits may also render it liable to carry the bacilli of anthrax should it have access to infected flesh.

(8) *Muscina (Cyrtoneura) stabulans* Fallen.

This common species is frequently found in and near houses. I have usually found it occurring with *H. canicularis* in the early summer (June) before *M. domestica* has appeared in any numbers. It is larger than *M. domestica*, and more robust in appearance. Its length varies from 7 to nearly 10 mm. Its general appearance is grey. The head is whitish-grey with a "shot" appearance. The frontal region of the male is velvety black and narrow; that of the female is blackish-brown, and is about a third of the width of the head. The bristle of the antenna bears setæ on the upper and lower sides. The dorsal side of the thorax is grey and has four longitudinal black lines; the scutellum is grey. The abdomen, as also the thorax, is really black covered with grey; in places it is tinged with brown, which gives the abdomen a blotched appearance. The legs are rather slender, and are reddish-gold or dirty orange and black in colour.

The eggs are laid upon the following substances, on which the larvæ feed: Decaying vegetable substances such as fungi, fruit, cucumbers, decaying vegetables, and they sometimes attack growing vegetables, having been introduced probably as larvæ with the manure, as they also feed on rotting dung and cow-dung. Howard (l. c.) found the fly frequenting human excrement, and observed the species breeding in the same. In the United States it has been reared from the pupæ of the cotton-worm and the gipsy moth; Riley was of the opinion that in the first case it fed on the rotten pupæ only. In 1891 it was also reared on the masses of larvæ and pupæ of the elm-leaf beetle. Other observers record it as being reared from the pupæ of such Hymenoptera as *Lophyrus*. In all these cases of its occurrence in the pupæ of insects, it

is difficult to say whether it is parasitic or whether it feeds on the rotting pupæ only; many observers are inclined to take the last view. The larva may reach a length of 11 mm. It is creamy-white in colour; the anterior spiracular processes are five-lobed and are like hands from which the fingers have been amputated at the first joint. The posterior spiracles are rounded and enclose three triangular-shaped areas, each containing a slit-like aperture. I have not been able to study the complete life-history, but Taschenberg (l. c.) states that it occupies five or six weeks.

#### (9) *Lucilia Cæsar* L.

Although it is not a house-fly, this common fly occasionally occurs in houses, especially those in the country, and it is often called a "blue-bottle." It is smaller than *C. erythrocephala* and is more brilliant in colouring, being of a burnished gold, sometimes bluish, and also of a shining green colour.

It frequents the excrement of man and other animals in which it is able to breed. Howard (l. c.) reared it from human excrement. It also breeds in carrion, but the chief breeding-place in which I have found it in this country is on the backs of sheep. It is one of the destructive species of "maggots" of sheep. The larvæ are very similar to those of *C. erythrocephala*—in fact, Portchinski considered them indistinguishable from the larvæ of the latter except in size. The full-grown larva measures 10–11 mm. in length. The larval life lasts about fourteen days, and the pupal stage a similar length of time, but I have reason to believe that under very favourable conditions development may take place in a much shorter time.

#### (10) *Psychoda* spp.

There may be found frequently on window-panes small, grey, moth-like flies belonging to the family *Psychodidæ*. The wings of these small flies are large and broad in proportion to the size of the body, and are densely covered with hair; when the insect is at rest they slope in a roof-like

manner. The larvæ of some species breed in human and other excrement, others breed in decaying vegetable substances, while certain species breed in water, especially when polluted with sewage, and these aquatic species have the spiracular apparatus modified accordingly. Although a form, *Phlebotomus*, which occurs in Southern Europe, has blood-sucking habits, the British species have no such annoying habits, and are of little importance in their relation to man.

#### IV. PHYSIOLOGY.

##### 1. The Influence of Food, Temperature, and Light.

Food.—Mention has already been made in the second part of this work of the influence of food on the development of the larvæ; the experiments which were carried out showed that the larvæ develop more rapidly in certain kinds of food, such as horse-manure, than in others. It has yet to be discovered what are the chemical constituents which favour the more rapid development. It was found that insufficient food in the larval state retarded development and produced flies which were subnormal in size. Bogdanow (1908), in an interesting experiment, fed *M. domestica* through ten generations on unaccustomed food such as meat and tanacetum in different proportions, and he found that the resulting flies did not show any change.

Temperature.—The influence of temperature on the development of the larvæ has been shown also. A high temperature accelerates the development of the egg, larva and pupa. Temperature also affects the adult insect; they are most active at a high summer temperature, and cold produces an inactive and torpid condition. They are able, however, to withstand a comparatively low temperature. Bachmetjew (1906) was able to submit *M. domestica* to as low a temperature as  $-10^{\circ}$  C., and vitality was retained, as they recovered when brought into ordinary room temperature. Donhoff (1872) performed a number of experiments previous

to this with interesting results. He submitted *M. domestica* for five hours to a temperature of  $-1.5^{\circ}$  C., and they continued to move. Exposed for eight hours to a temperature of first  $-3^{\circ}$  C. and then  $-2^{\circ}$  C. they moved their legs. On being submitted for twelve hours to a temperature first of  $-3.7^{\circ}$  C. and then  $-6.3^{\circ}$  C., they appeared to be dead, but on being warmed they recovered. When exposed for three hours to a temperature of  $-10^{\circ}$  C. which was then raised to  $-6^{\circ}$  C., they died. These experiments show that *M. domestica* is able to withstand a comparatively low degree of temperature.

Light.—The female of *M. domestica* deposits the eggs in dark crevices of the substance chosen for the larval nidus and as far away from the light as possible. Béclard (1858) showed that the eggs develop more quickly under blue and violet glass than under red, yellow, green, or white. The larvæ are negatively heliotropic, as Loeb (1890) has also proved in the larvæ of the blow-fly. As I have previously shown, the distinction between light and darkness is probably appreciated by the larvæ by means of the sensory tubercles of the oral lobes.

## 2. Hibernation.

This question is intimately connected with the preceding physiological facts. The disappearance of the flies towards the end of October and in November is a well-known fact, and an endeavour to discover the reason for this has been made in the present investigation.

I have found that the majority of flies observed were killed off by the fungus *Empusa muscæ* Cohn which is described in the present paper. Of the remainder some hibernate and some die naturally. This natural death may be compared, I think, to the like phenomenon that occurs in the case of the hive-bee *Apis mellifica*, where many of the workers die at the end of the season by reason of the fact that they are simply worn out, their function having been fulfilled. The flies which die naturally have probably lived for many



weeks or months during the summer and autumn, and in the case of the females have deposited many batches of eggs; their life work, therefore, is complete. Those flies which hibernate are, I believe, the most recently emerged, and therefore the youngest and most vigorous. On dissection it is found that the abdomens of these hibernating individuals are packed with fat cells, the fat body having developed enormously. The alimentary canal shrinks correspondingly and occupies a very small space; this is rendered possible by the fact that the fly does not take food during this period. In some females it was found that the ovaries were very well developed, while in others they were small, and mature spermatozoa were found in the males. Like most animals in hibernating, *M. domestica* becomes negatively heliotropic and creeps away into a dark place. In houses they have been found in various kinds of crevices such as occur between the woodwork and the walls. A favourite place for hibernation is between wall-paper which is slightly loose and the wall. A certain number hibernate in stables, where, owing to the warmth, they do not become so inactive, and they emerge earlier at the latter end of spring. During the winter the hibernating flies are sustained by means of the contents of the fat body, which is found to be extremely small in hibernating flies if dissected when they first emerge in May and June. The abdominal cavity is at first considerably decreased in size, but the fly begins to feed and soon the alimentary tract regains its normal size, and, together with the development of the reproductive organs, causes the abdomen to regain its normal appearance. The emergence from hibernation appears to be controlled by temperature, as one may frequently find odd flies emerging from their winter quarters on exceptionally warm days in the early months of the year (see Appendix).

### 3. Flight.

The distance that *M. domestica* is able to fly is one of practical importance in connection with their breeding habits



and disease-germ-carrying powers. Normally they do not fly great distances. They may be compared to domestic pigeons which hover about a house and the immediate neighbourhood. On sunny days they may be found in large numbers out-of-doors, but they retire into the houses when it becomes dull or rains. They are able to fly, however, a considerable distance, and can be carried by the wind. A few years ago, when visiting the Channel Islands, I found *M. domestica* from  $1\frac{1}{2}$  to 2 miles from any house or any likely breeding-place, so far as I was able to discover. Dr. M. B. Arnold has made some exact experiments at the Monsall Fever Hospital, Manchester, on the distance travelled by flies.<sup>1</sup> Three hundred flies were captured alive, and marked with a spot of white enamel on the back of the thorax. These were liberated in fine weather. Out of the 300 five were recovered in fly-traps at distances varying from 30 to 190 yards from the place of liberation, and all the recoveries were within five days. *M. domestica* is also able to fly at a considerable height above ground, and I have found them flying at an altitude of 80 feet above the ground. Such a height would greatly facilitate their carriage by the wind.

#### 4. Regeneration of Lost Parts.

If the wings or legs of *M. domestica* are broken off they do not appear to be able to regenerate the missing portions, as in the case of some insects, notably certain Orthoptera. Kammerer (1908), however, experimenting with *M. domestica* and *C. vomitoria*, has found that if the wing is extirpated from a recently pupated fly it is occasionally regenerated. The new wing is at first homogeneous, and contains no veins, but these appear subsequently.

<sup>1</sup> Recorded on p. 262 of the 'Report on the Health of the City of Manchester for 1906,' by James Niven, 1907.

## V. NATURAL ENEMIES AND OCCASIONAL PARASITES.

The most important of all the natural enemies of *M. domestica* is the parasitic fungus *Empusa muscæ*, which will be described here; this is the most potent of the natural means of destruction. Of animals, apart from the higher animals such as birds, spiders probably account for the greatest number, though owing to the normally clean condition of the modern house these enemies of the house-fly are refused admittance. I have been unable to rear any insect parasites, such as ichneumonids, from *M. domestica*. Their life indoors and the cryptic habits of the larvæ no doubt save them from the attacks of such insects; but Packard (1874) records the occurrence of the pupa of what was probably a Dermestid beetle, which he figures; this was found in a pupa of *M. domestica*. Predatory beetles and their larvæ probably destroy the larvæ, and Berg (1898) states that a species of beetle, *Trox suberosus* F., known as "Champi" in S. America, is an indirect destructor of the common fly. I have frequently observed the common wasp, *Vespa germanica*, seize *M. domestica* and carry it away. In some places in India it is the custom, so I have been told by residents, to employ a species of Mantis, one of the predatory "praying insects," to destroy the house-flies.

In view of the fact that the Arachnids *Chernes nodosus* and the species of Gamasid are occasionally found actually attached in a firm manner to *M. domestica*, they will be described under this head, but it must be clearly understood that it is still an open question whether they are external parasites in the true sense of the word, or whether *M. domestica*, instead of being the host, is merely the transporting agent as it appears to be in the majority of cases. For the present they may be termed for convenience "occasional parasites," in view of the fact that they have been found occasionally feeding upon *M. domestica*.

1. *Chernes nodosus* Schrank.

There are frequently found attached to the legs of the house-fly small scorpion or lobster-like creatures which are Arachnids belonging to the order Pseudo-scorpionidea; the term "chelifers" is also applied to them on account of the large pair of chelate appendages which they bear. The species which is usually found attached to *M. domestica* is *Chernes nodosus* Schrank (fig. 13). It is very widely distributed, and my observations agree with those of Pickard-Cambridge (1892), who has described the group.

The species is 2.5 mm. in length and Pickard-Cambridge's description of it is as follows:

"Cephalothorax and palpi yellowish red-brown, the former rather duller than the latter. Abdominal segments yellow-brown; legs paler. The caput and first segment of the thorax are of equal width (from back to front); the second segment of the thorax is very narrow. The surface of the cephalothorax and abdominal segments is very finely shagreened, the latter granulose on the sides. The hairs on this part as well as on the palpi and abdomen are simple, but obtuse. The palpi are rather short and strong. The axillary joint is considerably and somewhat subconically protuberant above as well as protuberant near its base underneath. The humeral joint at its widest part, behind, is considerably less broad than long; the cubital joint is very tumid on its inner side; the bulb of the pincers is distinctly longer, to the base of the fixed claw, than its width behind; and the claws are slightly curved and equal to the bulb in length."

They appear to be commoner in some years than in others. Godfrey (1909) says: "The ordinary habitat of *Ch. nodosus*, as Mr. Wallis Kew has pointed out to me, appears to be among refuse, that is, accumulations of decaying vegetation, manure-heaps, frames and hot-beds in gardens. He refers to its occurrence in a manure-heap in the open air at Lille, and draws my attention to its abundance in a melon-frame near Hastings in 1898, where it was found by Mr. W. R. Butterfield." In

view of these facts it is not difficult to understand its frequent occurrence on the legs of flies, which may have been on the rubbish heaps either for the purpose of laying eggs, or, what is more likely, because they have recently emerged from pupæ in those places and in crawling about, during the process of drying their wings, etc., their legs were seized by the *C. nodosus*.

The inter-relation of the *Chernes* and *M. domestica*, however, is one of no little complexity; much has been written and many diverse views are held concerning it. An interesting historical account of the occurrences of these Arachnids on various insects has been given by Kew (1901). Three views are held in explanation of the association and they are briefly these: First, that the *Chernes*, by clinging passively to the fly, uses it as a means of transmission and distribution; second, that the Arachnid is predaceous; and third, that it is parasitic on the fly. Owing to the unfortunate absence of convincing experimental proof in favour of either of the last two opinions, it is practically impossible to give any definite opinion as to the validity of these views; nevertheless they are worthy of examination.

The dispersal theory was held by Pickard-Cambridge and Moniez (1894). Whether the other views are held or not there is no doubt that such an association, even if it were only accidental, would result in a wider distribution of the species of *Chernes*, as the flies are constantly visiting fresh places suitable as a habitat for the same. Except in one or two recorded cases the Arachnids are always attached to the legs of the fly, the chitin of which is hard and could not be pierced, a fact which is held in support of this theory as the only explanation of the association.

The parasitic and predaceous views are closely related. The *Pseudo-scorpionidea* feed upon small insects, which they seize with their chelæ. It is suggested by some that the *Chernes* seizes the legs of the fly without realising the size of the latter. Notwithstanding its size, however, they remain attached until the fly dies and then feed upon the

body. In some cases as many as ten of the Arachnids have been found on a single fly, and if the movements of the insect are impeded by the presence of a number of the Chernes it will be easily understood that the life of the fly will be curtailed thereby. Pseudo-scorpionidea have been observed feeding on the mites that infest certain species of Coleoptera, and it has been suggested that they associated with the flies for the same purpose, although I do not know of any recorded case of a fly infested with mites carrying Chernes also. If this were the case the Chernes would be a friend and not a foe of the fly, as Hickson (1905) has pointed out.

There are few records to support the view that the Chernes is parasitic on the fly. Donovan (1797) mentions the occurrence of a pseudo-scorpionid on the body of a blow-fly, and Kirby and Spence (1826) refer to their being occasionally parasitic on flies, especially the blow-fly, under the wings of which they fix themselves. It is probable that the Chernes seldom reaches such a position of comparative security on the thorax of the fly; should it succeed in doing so, however, it could become parasitic in the true sense of the word. As I have previously pointed out, little experimental evidence is at present available and further investigation is necessary before it is possible to maintain more than a tentative opinion with regard to this association between the Chernes and the fly. It is obvious that the association will result in the distribution of the Pseudo-scorpionid, but whether this is merely incidental and the real meaning lies in a parasitic or predaceous intention on the part of the Arachnid, as some of the observations appear to indicate, further experiments alone will show.

## 2. Acarina or Mites borne by House-flies.

As early as 1735 de Geer observed small reddish Acari in large numbers on the head and neck of *M. domestica*. They ran about actively when touched. The body of this mite was oval in shape, completely chitinised, and polished;

the dorsal side was convex and the ventral side flat. Linnæus (1758) called this mite *Acarus muscarum* from de Geer's description, and Geoffroy (1764) found what appears to be the same, or an allied species of, mite, which he called the "brown fly-mite." Murray (1877) describes a form, *Trombidium parasiticum*,<sup>1</sup> which is a minute blood-red mite parasitic on the house-fly. He says: "In this country they do not seem so prevalent, but Mr. Riley mentions that in North America, in some seasons, scarcely a fly can be caught that is not infested with a number of them clinging tenaciously round the base of the wings." As it only possessed six legs it was doubtless a larval form.

Anyone who has collected Diptera as they have emerged from such breeding-places as hot-beds, rubbish and manure heaps will have noticed the frequently large number of these insects which are to be found carrying immature forms of the Acari. These are being transported merely by the flies in the majority of cases. Mr. Michael tells me that he used to call such flies "the emigrant waggons"—a very descriptive term. Many of these mites belong to the group *Gamasidæ*—the super-family *Gamasoidea* of Banks (1905). These mites have usually a hard coriaceous integument. In shape they are flat and broad and have rather stout legs. Sometimes immature forms of these mites swarm on flies emerging from rubbish heaps. Banks holds the opinion that they are not parasitic, but that the insect is only used as a means of transportation. It is difficult to decide whether this is so in all cases. I have illustrated (fig. 14) a specimen of the small house-fly, *H. canicularis*, caught in a room; on the under-side of the fly's abdomen a number of immature *Gamasids*<sup>2</sup> are attached,

<sup>1</sup> This species was named *Atoma parasiticum* and later *Astoma parasiticum* by Latreille ('Magazin Encyclopedique,' vol. iv, p. 15, 1795). Mr. A. D. Michael tells me that the genus was founded on *Trombidium parasiticum* of de Geer. They were really larval *Trombidiidæ* and *Atoma* was founded on larval characters; probably any larval *Trombidium* came under the specific name.

<sup>2</sup> Being unable to identify these immature specimens I submitted them to Mr. Michael, who kindly informs me that it is extremely diffi-



apparently by their stomal regions. These specimens may be truly parasitic, as I am inclined to believe, since many Acari are parasitic in the immature state, although the adults may not be so; on the other hand this form of attachment may be employed as a means of maintaining a more secure hold of the transporting insect.

### 3. Fungal Disease—*Empusa muscæ* Cohn.

Towards the end of the summer large numbers of flies may be found attached in a rigid condition to the ceiling, walls or window-panes. They have an extremely life-like appearance, and it is not until one examines them closely or has touched them that their inanimate, so far as the life of the fly is concerned, condition is discovered. These flies have been killed by the fungus *Empusa muscæ* Cohn, and in the later stages of the disease its fungal nature is recognised by the fact that a white ring of fungal spores may be seen around the fly on the substratum to which it is attached. The abdomen of the fly is swollen considerably, and white masses of sporogenous fungal hyphæ may be seen projecting for a short distance from the body of the fly, between the segments, giving the abdomen a transversely striped black and white appearance.

The majority of flies which die in the late autumn—and it is then that most of the flies which have been present during the summer months perish—are killed by this fungus. Its occurrence, therefore, is of no little economic value, especially if it were possible to artificially cultivate it and destroy the flies in the early summer instead of being compelled to wait until the autumn for the natural course of events.

*Empusa muscæ* belongs to the group Entomophthorææ, the members of which confine their attacks to insects, and in many cases, as in the case of the present species, are productive of great mortality among the individuals of the species of

cult to identify immature Gamasids owing to the scarcity of knowledge as to their life-histories, but he says that they are very like *Dinychella asperata* Berl.



insect attacked. In this country it may be found from about the beginning of July to the end of October, and usually occurs indoors. It appears to be very uncommon out-of-doors. A case has been recently recorded<sup>1</sup> of its occurrence on Esher Common, where it had attacked a species of Syrphid, *Melanostomum scalare* Fabr. Thaxter (1888) also mentions two cases of its occurrence out-of-doors in America, in both of which cases it had attacked, singularly enough, species of Syrphidæ. This author states that *Empusa muscæ* is probably the only species which occurs in flowers attractive to insects, but he only observed it on the flowers of *Solidago* and certain Umbellifereæ.

The development of this species was studied by Brefeld (1871). An *Empusa* spore which has fallen on a fly rests among the hairs covering the insect's body and there adheres. A small germinating hypha develops, which pierces the chitin, and after entering the body of the victim penetrates the fat-body. In this situation, which remains the chief centre of development, it gives rise to small spherical structures which germinate in the same manner as yeast cells, forming gemmæ. These separate as they are formed, and falling into the blood sinus are carried throughout the whole of the body of the fly. It was probably these bodies that Cohn (1855) found, and he explained their presence as being due to spontaneous generation; he believed that the fly first became diseased and that the fungus followed in consequence. After a period of two or three days the fly's body will be found to be completely penetrated by the fungus, which destroys all the internal tissues and organs. The whole body is filled with the gemmæ, which germinate and produce ramifying hyphæ (fig. 15). The latter pierce the softer portions of the body-wall between the segments and produce the short, stout conidiophores (*c.*), which are closely packed together in a palisade-like mass to form a compact white cushion of conidiophores, which is the transverse white ring that one finds between each of the segments of a diseased, and

<sup>1</sup> 'Trans. Ent. Soc. London,' 1908 ("Proceedings," p. 57).

consequently deceased, fly. A conidium now develops (fig. 16) by the constriction of the apical region of the conidiophore. When it is ripe the conidium (fig. 17) is usually bell-shaped, measuring 25–30  $\mu$  in length; it generally contains a single oil-globule (*o.g.*). In a remarkable manner it is now shot off from the conidiophore, often for a distance of about a centimetre, and in this way the ring or halo of white spores, which are seen around the dead fly, are formed. In some cases, although I find that it is not an invariable rule as some would suggest, the fly, when dead, is attached by its extended proboscis to the substratum. Giard (1879) found that blow-flies killed by *Entomophthora calliphora* were attached by the posterior end of the body. If the conidia, having been shot off, do not encounter another fly, they have the power of producing a small conidiophore, upon which another conidium is in turn developed and discharged. If this is unsuccessful in reaching a fly a third conidium may be produced, and so on. By this peculiar arrangement the conidia may eventually travel some distance, and it is no doubt a great factor in the wide distribution of the fungus, once it occurs. On the fly itself short conidiophores may be found producing secondary conidia.

Reproduction by conidia appears to be the only form of generation, as we are still uncertain as to the occurrence of a resting-spore stage in this species. Winter (1881) states that he found resting-spores in specimens of *M. domestica* occurring indoors; they also produced conidia which he identified as *E. muscæ*. These azygospores measured 30–50  $\mu$  in diameter, and were produced laterally or terminally from hyphæ within the infected fly. Giard (*l. c.*) describes resting spores which were produced externally and on specimens found in cool situations. Brefeld, however, is of the opinion that *E. muscæ* does not produce resting-spores. The question of the production of resting-spores needs further investigation, as it is one of some importance. In the absence of confirmatory evidence it is extremely difficult to understand how the gap in the history of the *Empusa*, between the

late autumn of one year and the summer of the next, is filled. A number of suggestions have been made, many of which cannot be accepted; for example, Brefeld believes that the *Empusa* is continued over the winter in warmer regions, migrating northwards with the flies on the return of summer! In the case of *Entomophthora calliphora*, Giard believes that the cycle is completed by the corpses of the blow-flies falling to the ground, when the spores might germinate in the spring and give rise to conidia which infect the larvæ. Olive (1906) studied the species of *Empusa* which attacks a species of *Sciara* (Diptera) and found the larvæ infected. He accordingly thinks that the disease may be carried over the winter by those individuals which breed during that period in stables and other favourable places. As I have shown, *M. domestica*, under such favourable conditions as warmth and supply of suitable larval food, is able to breed during the winter months, although it is not a normal occurrence so far as I have been able to discover. If, then, these winter-produced larvæ could become infected they might assist in carrying over the fungus from one year to the next, and thus carry on the infection to the early summer broods of flies. This suggestion and the possible occurrence of a resting-spore stage appears to me to be the probable means by which the disease may be carried over from one "fly-season" to the next.

*E. muscæ*, besides occurring in *M. domestica*, has been found on several species of *Syrphidæ*, upon which it usually occurs out-of-doors, as I have already mentioned. In addition to these Thaxter records its occurrence in *Lucilia cæsar* and *Calliphora vomitoria*.

## VI. TRUE PARASITES.

### 1. Flagellata. *Herpetomonas muscæ-domesticæ* Burnett.

This flagellate has been known as a parasite of the alimentary tract of *M. domestica* for many years. Stein (1878) figures a flagellate which he calls *Cercomonas muscæ-domestica*, and identifies it with the *Bodo muscæ-*

*domesticæ* described by Burnett and the *Cercomonas muscarum* of Leidy. For this form figured by Stein, a new genus, *Herpetomonas*, was instituted by Kent (1880-81), and it is taken as the type-species. It was not until the economic importance of certain of the hæmo-flagellates was recognised that other flagellates, including *H. muscæ-domesticæ*, received further attention, and then Prowazek (1904) described with great detail the development of this species. In the previous year Léger (1903) had given a short account of it, and since Prowazek's memoir Patton (1908, 1909) has given short preliminary accounts of his study of the life-history. The accounts of both these authors differ in several respects from that of Prowazek, as will be shown. I have examined a very large number of the contents of English specimens of *M. domestica*, but, with one or two doubtful exceptions, unfortunately I have been unable so far to discover any of these flagellates in my film preparations.

The full-grown flagellate (VIII) measures 30-50  $\mu$  in length. The body is flattened and lancet-shaped, the posterior end being pointed and the anterior end bluntly rounded. The alveolar endoplasm contains two nuclear structures. In the centre is the large "trophonucleus" (*tr.*); it contains granules of chromatin, but is sometimes difficult to see. Near the anterior end the deeply staining rod-shaped "kinetonucleus" (blepharoplast of many authors) (*k.*) lies, usually in a transverse position. The single stout flagellum, which is a little longer than the body of the flagellate, arises from the anterior end, near the kinetonucleus. Prowazek describes the flagellum as being of a double nature and having a double origin; this, which is a mistaken interpretation, is repeated by Lingard and Jennings (1906).

This mistake, as pointed out by Léger and Patton, is due to the fact that the majority of the adult flagellates have the appearance of a double flagellum, which represents the beginning of the longitudinal division of the flagellate (VI). Patton (1908) figures a stage in *H. lygæi* with the double flagellum, and Léger (1902) in a similar stage in *H. jaculum*,

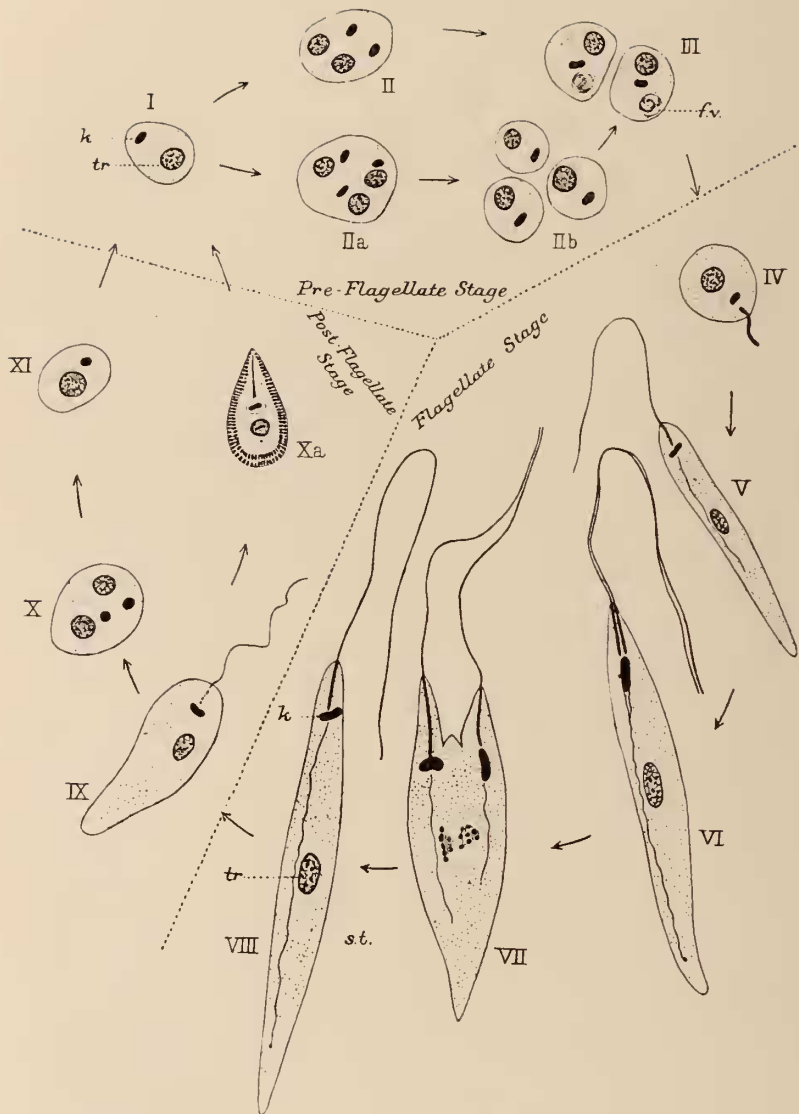


Diagram of the life-cycle of *Herpetomonas muscæ-domestica* Burnett. Arrangement chiefly after Patton; figures after Léger, Patton, and Prowazek. I-III. Preflagellate stage. IV-VIII. Flagellate stage: V. Young flagellate. VI. Flagellate beginning to divide, flagellum having already divided. VII. Advanced stage of division. VIII. Adult flagellate. IX-XI. Post-flagellate stage: IX. Degeneration of flagellum. Xa. Post-flagellate stage completed by formation of gelatinous covering, containing double row of granular bodies (Prowazek). *f.v.* Flagellar vacuole. *k.* Kinetoplast. *st.* Spiral chromophilous thread. *tr.* Trichonucleus.

parasitic in the gut of *Nepa cinerea*, from which figures it may be understood how the mistake has arisen. Through this misinterpretation Prowazek was led to consider that the parasite was of a bipolar type, in which the body had been doubled on itself so that the two ends came together and the flagellum remained distinct. The flagellum, according to Léger, is continued into the cytoplasm as a thin thread, which stains with difficulty, and terminates in a double granule above the kintonucleus; this double granule is no doubt the "diplosome" of Prowazek. According to the latter author another deeply staining double thread (*s.t.*), that appears to be spirally coiled, runs backwards from the kintonucleus and terminates posteriorly in a distinct granule, shown in fig. VIII.

The flagellates congregate in the proventriculus or in the posterior region of the intestine, where they become united by their anterior ends to form rosettes. Prowazek states that in the rosette condition the living portion of the flagellate resides, as it were, in the long tail-like process.

Patton divides the life-cycle of *H. muscæ-domestica* into three stages—the preflagellate, flagellate, and post-flagellate. The last two are common, but the first stage is not common, and Prowazek appears to have overlooked it. For convenience I have described the flagellate stage first, and the process of division in this stage is simple longitudinal fusion. The nuclei divide independently, and the kintonucleus usually precedes the trophonucleus. The latter undergoes a primitive type of mitosis, in which Prowazek recognised eight chromosomes (VII). The flagellum divides longitudinally, and each of the two halves of the kintonucleus appropriates one of the halves with its basal granule.

The preflagellate stage, which Patton (1909) describes, usually occurs in the masses which lie within the peritrophic membrane.<sup>1</sup> They are round or slightly oval bodies (I), their average breadth being 5.5  $\mu$ . The protoplasm is granular and

<sup>1</sup> I assume that Patton refers to this membrane by the term "peritricheal membrane."



contains a trophonucleus and kinetonucleus. Division takes place by simple longitudinal division or multiple segmentation, and in this manner a large number of individuals are formed (II *b* and III). These develop into the flagellate stage: a vacuole, the flagellar vacuole (III, *f.v.*) appears between the kinetonucleus and the rounded end of the pre-flagellate form, and in it the flagellum appears as a single coiled thread, which is extended when the vacuole has approached the surface.

The flagellate form has already been described, and in the concluding portion of the flagellate stage, which, according to Prowazek, is found in starved flies, these forms are found collecting in the rectal region, and attaching themselves by their flagellar ends in rows to gut epithelium. The more external ones begin to shorten, during which process the flagella degenerate (IX) and are shed. Thus a palisade of parasites is formed, the outer ones being rounded and devoid of flagella, and some of them may be found dividing (X). Léger (1902) terms these the "formes grégariennes," and maintains that the existence of these "gregarine" forms is a powerful argument in favour of the flagellate origin of the Sporozoa, which he had previously suggested, and which Bütschli had put forward in 1884. After the degeneration of the flagellum a thickened gelatinous covering is formed, containing a double row of granular bodies (Xa), and these cysts are regarded by Patten as the post-flagellate stage. They pass out with the fæces, and dropping on the moist window-pane or on food, are taken up by the proboscides of other flies.

Prowazek describes dimorphic forms of the flagellate stage, which he regards as sexually differentiated forms, but Patton, in a letter to me, says that he is unable to find any of these complicated sexual stages. According to Prowazek, one of these forms is slightly larger than the other, and has a greater affinity for stain. The dimorphic forms conjugate; their cell substance and nuclei fuse, and a resting-stage cyst is formed, but the subsequent stages have not been followed. He further states that the sexually differentiated forms may force



their way into the ovaries, where they undergo autogamy and infect the subsequent brood.

In Madras Patton found that 100 per cent. of the flies were infected with the flagellate; Prowazek found it in 8 per cent. of the flies at Rovigno. In the cold season in the plains (India) Lingard and Jennings (l. c.) found the flagellate in less than 1 per cent. of the flies examined; in the hills (Himalayas), at an elevation of 7500 feet, the flagellates were most numerous during the hottest season of the year, and gradually decreased in number to October and November, when none were discovered.

One of the chief points of interest in connection with this flagellate is its similarity to the "Leishmann-Donovan" body, the parasite of kala-azar, as it was this resemblance that prompted Rogers (1905) to suggest that the latter parasite was a *Herpetomonas*, which I think Patton has now conclusively proved to be the case, and he calls it *Herpetomonas donovani* (Laveran and Mesnil).

#### *Crithidia Muscæ-domesticæ* Werner.

This parasite has been recently described by Werner (1908), who found it in the alimentary tracts of four out of eighty-two flies. It measures 10–13  $\mu$  in length, the length of the body being 5–7  $\mu$  and the flagellum 5–6  $\mu$ . As in other members of the genus *Crithidia*, which is closely allied to *Herpetomonas*, the breadth of the body is great compared with the length, and the kinetonucleus and trophonucleus are rather close together. A short, staining, rod-like body lies between the kinetonucleus and the base of the flagellum. The flagellum is single. Dividing forms undergoing longitudinal division were frequently found. The kinetonucleus appears to divide first, followed in succession by the flagellum and the trophonucleus. Forms undergoing division and showing a single trophonucleus and double kinetonucleus and flagellum were also found. Cases occurred in which the fission began at the

non-flagellate end of the body. No conjugating forms were found, nor any wandering into the ovaries.

Lingard and Jennings (l. c.) describe certain flagellates of a flag-shaped or rhomboidal nature, which I am strongly of the opinion are species of *Crithidia* and not species of *Herpetomonas*. Closely following Prowazek's account of *H. muscæ-domesticæ* they describe and figure all their forms as having two flagellæ in the flagellate stage. If one allows for the rupture of the flagellum from the bodies of the organism in making the film, some of their figures are not unlike those of *Crithidia gerridis*, parasitic in the alimentary tract of an Indian water-bug, *Gerris fossarum* Fabr., and described by Patton (1908).

## 2. Nematoda—*Habronema muscæ* (Carter).

Carter (1861) appears to be the first to have described a parasitic worm in *M. domestica*. He described a bisexual nematode infesting this insect in Bombay, and found that: "Every third fly contains from two to twenty or more of these worms, which are chiefly congregated in, and confined to, the proboscis, though occasionally found among the soft tissues of the head and posterior part of the abdomen." His description of this nematode, to which he gave the name *Filaria muscæ*, is as follows: "Linear, cylindrical, faintly striated transversely, gradually diminishing towards the head, which is obtuse and furnished with four papillæ at a little distance from the mouth, two above and two below; diminishing also towards the tail, which is short and terminated by a dilated round extremity covered with short spines. Mouth in the centre of the anterior extremity. Anal orifice at the root of the tail." He gives the length as being one eleventh of an inch and the breadth as one three hundred and thirteenth of an inch. In his description of his figures of the worm he calls what is evidently the anterior region of the intestine the "liver." Von Linstow (1875) described a small nematode, which he calls *Filaria stomoxeos*, from the

head of *S. calcitrans*; this larva measured 1.6 to 2 mm. in length. Generali (1886) described a nematode from the common fly, which he calls *Nematodum spec.* It is highly probable, as my friend Dr. A. E. Shipley has suggested to me, that Generali's nematode and the *F. muscæ* of Carter are identical. Diesing (1861) created the genus *Habronema* for the *Filaria muscæ* of Carter, and his description is practically a translation of Carter's original description. Piana (1896) describes a nematode from the proboscis of *M. domestica*, which, in the occurrence of the male and female genital organs in the same individual, he says, resembles Carter's nematode. He finds that at certain seasons of the year and in certain localities it is very rare, while at others it may occur in 20-30 per cent. of the flies. The larva, after fixation, measured 2.68 mm. in length and 0.08 mm. in breadth. It was cylindrical and gently tapering off at the extremities, with the mouth terminal.

Out of the many hundreds of flies which I have dissected I have only found two specimens of this nematode (fig. 18). From the descriptions given by Carter and Piana and the figures of the latter I feel convinced that their specimens and mine are the same species, called by Diesing *Habronema muscæ* (Carter). It is linear, cylindrical, tapering gradually towards both ends. The anterior end is slightly rounded, having the mouth in the centre. I am unable to confirm the presence of the four papillæ which Carter describes as a little distance from the mouth, nor are they figured by Piana. The cuticle is very faintly marked with transverse striations. The common genital and anal orifice is situated at a short distance from the posterior end of the body, which tapers off slightly more than the anterior end and terminates in a small dilated extremity, which is covered with minute spines (fig. 19). My specimens appear to be immature adult forms, not having reached sexual maturity. The species measures 2 mm. in length and 0.04 mm. in breadth. The specimens that I obtained were situated in the head region, between the optic ganglia and the cephalic air-sacs, from which position they

could easily move down into the cavity of the proboscis. I am unaware of any previous record of the occurrence of *Habronema muscæ* in this country, but I have no doubt that if one searched specially for it it would be found to occur more commonly than might appear from my experience, and to be generally distributed with its host throughout the world.

The occurrence of a parasitic worm in this position is of great interest, even though *M. domestica* is not a blood-sucking species and the nematode is not of the nature of *Filaria bancrofti*. There is no reason, however, why *M. domestica* should not under certain conditions carry pathogenic nematodes, which might easily get on to the food of man.

### 3. Dissemination of Parasitic Worms.

In this connection reference might be made to the experiments of Grassi (1883) to which reference is made by Nuttall in his valuable memoir (1899). Grassi broke up segments of *Tænia solium* in water; they had previously been preserved in alcohol for some time. Flies sucked up the eggs in the water and he found them unaltered in the fæces. *Oxyuris* eggs were also passed unaltered. In another experiment flies fed on the eggs of *Trichocephalus* and he found the eggs some hours afterwards in the flies' fæces, which had been deposited in the story beneath the laboratory; he also caught flies in this kitchen with their intestines full of eggs.

Calandruccio<sup>1</sup> examined flies (? species) which had settled upon fæces containing the ova of *Tænia nana*. The ova were found in the flies' intestines. The excrement deposited by a fly on sugar contained two or three ova of the *Tænia*. By means of such infected sugar a girl was infected, and ova of *T. nana* were found in her stools on the twenty-seventh day.

<sup>1</sup> "Ulteriori ricerche sulla *Tænia nana*," 'Boll. Soc. Zool. Ital. Roma,' vol. vii, pp. 65-69; also in 'Boll. Acad. Gioenia, Catania,' Fasc. 89, pp. 15-19.

Nuttall (l. c.) records a personal communication of Stiles, who placed the larvæ of *Musca* with female *Ascaris lumbricoides*, which they devoured together with the eggs contained by the nematodes. The larvæ and adult flies contained the eggs of the *Ascaris*, and as the weather at the time of the experiment was very hot the *Ascaris* eggs developed rapidly and were found in different stages of development in the insect, thus proving, as Nuttall points out, "that the latter may serve as disseminators of the parasite." These experiments of Grassi and Stiles show that flies can act as carriers of the eggs of these parasitic worms, and that man could be infected by the fly depositing its excreta on his food, or being accidentally immersed in food as flies frequently are.

#### VII. THE DISSEMINATION OF PATHOGENIC ORGANISMS BY *MUSCA DOMESTICA* AND ITS NON-BLOOD-SUCKING ALLIES.

Although *M. domestica* is unable to act as a carrier of pathogenic micro-organisms in a manner similar to that of the mosquito, so far as we know at present, nevertheless its habits render it a very potent factor in the dissemination of disease by the mechanical transference of the disease germs. These habits are the constant frequenting and liking for substances used by man for food on the one hand and excremental products, purulent discharges, and moist surfaces on the other. Should these last contain pathogenic bacilli, the proboscis, body, and legs of the fly are so densely setaceous (see fig. 20) that a great opportunity occurs, with a maximum amount of probability, for the transference of the organisms from the infected material to either articles of food or such moist places as the lips, eyes, etc. As I have already pointed out (1907), *M. domestica* is unable to pierce the skin, as certain persons have suggested. The structure of the proboscis will not permit the slightest piercing or pricking action, which fact eliminates such an inoculative method of infection. It is as a mechanical carrier, briefly, that *M.*

*domestica* and such allies as *H. canicularis*, etc., though to a less degree, may be responsible for the spread of infectious disease of a bacillary nature, and an account will now be given of the rôle which this insect plays in the dissemination of certain diseases.<sup>1</sup> Before doing so, however, it should be pointed out that whereas in some of the diseases the epidemiological evidence adduced in support of the transference of disease germs by flies is confirmed bacteriologically, in others only the former evidence exists. Should neither form of evidence be available in support of the idea that *M. domestica* plays a part in the dissemination of the infection of a particular disease, it is essential, nevertheless, that if such a method of transference is possible the potency of this insect should be realised. This potency is governed by such factors as the presence of *M. domestica*; its access to the infected or infective material, this being attractive to the insect either because it is moist or because it will serve as food for itself or its progeny; and a certain power of resistance for a short time against desiccation on the part of the pathogenic organisms, although, as in the case of the typhoid bacillus, the absence of this factor is not fatal to the idea, as it may be overcome by the fact that the fly is able to take on its appendages an amount sufficient to resist desiccation for a short time. The last factor is the presence of suitable culture media, such as certain foods, or moist surfaces as the mouth, eyes, or wounds, for the reception of the organisms which have been carried on the body or appendages of the fly. If these conditions are satisfied the possibility of *M. domestica* or its allies playing a part in the transference of the infection should be carefully considered, and this suggestive evidence will be discussed in certain of the diseases which follow, in addition to the epidemiological and bacteriological evidence.

<sup>1</sup> Though it should be unnecessary, I wish to explain, as I have been occasionally misunderstood by medical men and others, that *M. domestica* is not regarded as being the cause of any disease, but as a carrier of the infection.



### 1. Typhoid Fever.

Of all infectious diseases the conditions in this are most favourable for the transference of infection by *M. domestica*, and it is no doubt on this account that the greatest attention has been paid to the rôle of house-flies in the dissemination of this disease. The chief favourable condition is that the typhoid bacillus occurs in the stools of typhoid and incipient typhoid cases. Human excrement attracts flies not only on account of its moisture but as suitable food for the larvæ. The infected excrement is often accessible to flies, especially in military camps, as will be shown shortly, and the flies also frequent articles of food and not infrequently the moist lips of man. Such are the conditions most suitable for the transference of the bacilli, and it is on account of the frequent coincidence of these conditions that flies can play, and have played, such an important rôle in the dissemination of this disease among communities, in spite of the fact that the typhoid bacillus cannot survive desiccation, which I think is an argument against its being carried by dust.

Epidemiological and other evidence.—There is a very large amount of testimony given as to the rôle played by flies in the spread of enteric in military stations and camps, and especially during the two wars—the Spanish-American and the Boer War. All the conditions most favourable for the dissemination of the bacilli by flies were, and in many military stations are still, present; open latrines or filth-trenches accessible to flies on the one hand and on the other the man's food within a short distance of the latrines. I cannot do better than repeat the evidence in the words of the witnesses and allow it to speak for itself.

Vaughan, a member of the U.S. Army Typhoid Commission of 1898, states:<sup>1</sup>

“My reasons for believing that flies were active in the dissemination of typhoid fever may be stated as follows:

<sup>1</sup> In a paper, “Conclusions Reached after a Study of Typhoid Fever among American Soldiers,” read before the American Medical Association at Atlantic City, N.J., in 1900.

“(a) Flies swarmed over infected faecal matter in the pits and then visited and fed upon the food prepared for the soldiers in the mess-tents. In some instances where lime had recently been sprinkled over the contents of the pits, flies with their feet whitened with lime were seen walking over the food.

“(b) Officers whose mess-tents were protected by screens suffered proportionately less from typhoid fever than did those whose tents were not so protected.

“(c) Typhoid fever gradually disappeared in the fall of 1898 with the approach of cold weather and the consequent disabling of the fly.

“It is possible for the fly to carry the typhoid bacillus in two ways. In the first place faecal matter containing the typhoid germs may adhere to the fly and be mechanically transported. In the second place, it is possible that the typhoid bacillus may be carried in the digestive organs of the fly and may be deposited with its excrement.”

One of his conclusions was that infected water was not an important factor in the dissemination of typhoid in the national encampments of 1898, since only about one fifth of the soldiers in the national encampments during the summer of that year developed typhoid fever, whereas about 80 per cent. of the total deaths were due to this disease. In the latter connection Sternberg (1899) refers to a report of Dr. Reed upon an epidemic in the Cuban War, in which it was stated that the epidemic was clearly not due to water infection but was transferred from the infected stools of the patients to the food by means of flies, the conditions being especially favourable for this means of dissemination. Sternberg, as Surgeon-General of the U.S. Army, issued the following instructions<sup>1</sup>: “Sinks should be dug before a camp is occupied or as soon after as practicable. The surface of the faecal matter should be covered with fresh earth or quicklime or ashes three times a day.” I think that the instructions of that ancient leader of men, Moses, who probably had

<sup>1</sup> ‘Circular No. 1 of the Surgeon-General of the U.S. Army,’ April, 1898.

experienced the effects of flies, were even better than these. He said (Deut., Ch. xxiii, v. 12-13): "Thou shalt have a place also without the camp whither thou shalt go forth abroad; and thou shalt have a paddle [or 'shovel'] among thy weapons; and it shall be, when thou sittest down abroad, thou shalt dig therewith, and shalt turn back and cover that which cometh from thee."

Sternberg is of the opinion that typhoid fever and camp diarrhœa are frequently communicated to soldiers through the agency of flies, "which swarm about fæcal matter and filth of all kinds deposited upon the ground or in shallow pits, and directly convey infectious material attached to their feet or contained in their excreta to the food which is exposed while being prepared in the common kitchen, or while being served in the mess-tent."

Veeder (1898), in referring to the conditions existing in the camps of the Spanish-American war, says that in the latrine trenches he saw "fæcal matter fresh from the bowel and in its most dangerous condition, covered with myriads of flies, and at a short distance there was a tent, equally open to the air, for dining and cooking. To say that the flies were busy travelling back and from between these two places is putting it mildly." Further, he says, "There is no doubt that air and sunlight kill infection, if given time, but their very access gives opportunity for the flies to do serious mischief as conveyers of fresh infection wherever they put their feet. In a very few minutes they may load themselves with the dejections from a typhoid or dysenteric patient, not as yet sick enough to be in hospital or under observation, and carry the poison so taken up into the very midst of the food and water ready for use at the next meal. There is no long and round-about process involved. It is very plain and direct. Yet when the thousands of lives are at stake in this way the danger passes unnoticed, and the consequences are disastrous and seem mysterious until attention is directed to the point; then it becomes simple enough in all conscience."

The Commission which investigated the outbreaks of

enteric fever that occurred in 1898 in the United States during this war came to the conclusion that "flies undoubtedly served as carriers of the infection" under the conditions which have already been described. Many other authorities bear witness to the same facts.

In our own South African war, a year or two later, the same conditions existed, and there was a very heavy loss of life from enteric fever. Writing on the subject, Dunne (1902) says: "The plague of flies which was present during the epidemic of enteric at Bloemfontein in 1900 left a deep impression on my mind, and, as far as I can ascertain from published reports, on all who had experience on that occasion. Nothing was more noticeable than the fall in the admissions from enteric fever coincident with the killing off of the flies on the advent of the cold nights of May and June. In July, when I had occasion to visit Bloemfontein, the hospitals there were half empty, and had practically become convalescent camps." A similar experience is related by Tooth (1901). Referring to the rôle of flies he says: "As may be expected, the conditions in these large camps were particularly favourable to the growth and multiplication of flies, which soon became terrible pests. I was told by a resident in Bloemfontein that these insects were by no means a serious plague in ordinary times, but that they came with the army. It would be more correct to say that the normal number of flies was increased owing to the large quantities of refuse upon which they could feed and multiply. They were all over our food, and the roofs of our tents were at times black with them. It is not unreasonable to look upon flies as a very possible agency in the spreading of the disease, not only abroad but at home. It is a well-known fact that with the first appearance of the frost enteric fever almost rapidly disappears. . . . It seems hardly credible that the almost sudden cessation of an epidemic can be due to the effect of cold upon the enteric bacilli only. But there can be no doubt in the mind of anybody who has been living on the open veldt, as we have for three or four months, that flies are ex-

tremely sensitive to the change of temperature, and that the cold nights kill them off rapidly." In the discussion on this paper Church stated that "many nurses told me that if one went into a tent or ward in which the patients were suffering from a variety of diseases, one could tell at once which were the typhoid patients by the way in which the flies clustered about their mouths and eyes while in bed." It was further stated in the discussion that where the Americans used quicklime in their latrines the cooks in the neighbouring kitchens found that the food became covered with quicklime from the flies which came from the latrines to the kitchens.

Dr. Tooth, in a letter to me, says: "I am afraid my written remarks hardly express strongly enough the importance that I attach to flies as a medium of spreading infection. Of course I do not wish to under-rate the water side of the question, but once get, by that means, enteric into a camp the flies, in my opinion, are quite capable of converting a sporadic incidence into an epidemic. A pure water supply is an obvious necessity, but the prompt destruction of refuse of every description is every bit as important."

Smith (1903), in speaking of his experiences in South Africa, says that: "On visiting a deserted camp during the recent campaign it was common to find half a dozen or so open latrines containing a foetid mass of excreta and maggots." Similar observations were made by Austen (1904), who, describing a latrine that had been left a short time undisturbed, says: "A buzzing swarm of flies would suddenly arise from it with a noise faintly suggestive of the bursting of a percussion shrapnel shell. The latrine was certainly not more than one hundred yards from the nearest tents, if so much, and at meal-times men's mess-tins, etc., were always invaded by flies. A tin of jam incautiously left open for a few minutes became a seething mass of flies (chiefly *Pycnosoma chloropyga* Wied), completely covering the contents."

Howard (1900) referring to an American camp, where no effort was made to cover the faeces in the latrines, says: "The camp contained about 1200 men, and flies were extremely

numerous in and around the sinks. Eggs of *Musca domestica* were seen in large clusters on the *fæces*, and in some instances the patches were two inches wide and half an inch in depth, resembling little patches of lime. Some of the sinks were in a very dirty condition and had a very disagreeable odour."

A few examples of the prevalence of conditions favouring the dissemination of enteric by flies in permanent camps may be noted. Cockerill (1905), in describing camp conditions in Bermuda, mentions kitchens within one hundred yards of the latrines; the shallow privy, seldom or never cleaned out, and middens are found which contain masses of filth swarming with flies. He states that in more recent years the period of greatest incidence is in the summer, being chiefly due to flies and contaminated dust. Quill (1900), reporting on an outbreak of enteric in the Boer camp in Ceylon, states: "During the whole period that enteric fever was rife in the Boer camp flies in that camp amounted to almost a plague, the military camp being similarly infested, though to a less extent. The outbreak in the Boer camp preceded that among the troops; the two camps were adjacent, and the migration of the flies from the one to the other easy." Weir, reporting on an outbreak of enteric fever in the barracks at Umbala, India,<sup>1</sup> says that most of the pans in the latrines were half or quite full, and flies were very numerous in them and on the seats, which latter were soiled by the excreta conveyed by the flies' legs. The men stated that the plague of flies was so great that in the morning they could hardly go to the latrines. He found that the flies were carried from the latrines to the barrack-rooms on the clothes of the men. This state of affairs suggests another mode of infection, namely, *per rectum*. As Smith has pointed out (*l.c.*) it is not improbable that flies under these conditions may be inoculators of dysentery.

Aldridge (1907) gives some interesting statistics showing the influence of the presence of breeding-places of flies. Flies are found in greater numbers in mounted regiments than in

<sup>1</sup> 'Army Medical Department Report,' 1902, p. 207.



infantry, and he shows how this affects the incidence of enteric fever. In the British Army in India, 1902-05, the ratios per 1000 per annum of cases admitted were: cavalry 41.1, and infantry 15.5; and in the U.S. Army were: cavalry 5.74, and infantry 4.75. He states that: "A study of the incidence of enteric fever shows that stations where there are no filth trenches, or where they are a considerable distance from the barracks, all have an admission-rate below the average, and all but one less than half the average."

All these facts are equally applicable to the conditions in our own towns and cities. Where the old conservancy methods are used, such as pails and privy middens, the incidence of typhoid fever is greater than in those places where the system of water disposal has been adopted. I have examined the annual reports of the medical officers of health of several large towns where such conversions are being made, and they show a falling-off of the typhoid fever-rate coincident with this change. In Nottingham, for example,<sup>1</sup> in the ten years 1887-1896, there was one case of typhoid fever for every 120 houses that had pail-closets, one case for every 37 houses with privy middens, and one case for every 5.58 houses with water-closets. The last were scattered, and not confined to the prosperous districts of the town.

One of the most important investigations on the relation of flies to intestinal disease was that of Jackson (1907). He investigated the sanitary condition of New York harbour and found that in many places sewer outfalls had not been carried below low-water mark, consequently solid matter from the sewers was exposed on the shores, and that during the summer months on and near the majority of the docks in the city a large amount of human excreta was deposited. This was found to be covered with flies. The report, considered as a mere catalogue, is a most severe indictment against the insanitary condition of this great water front. By means of spot-maps he shows that the cases of typhoid are thickest

<sup>1</sup> "Typhoid Fever and the Pail System at Nottingham," 'Lancet,' November 29th, 1902, p. 1489.

near the points found to be most insanitary. He shows, as English investigators have also shown, how the curves of fatal cases correspond with the temperature curves and with the curves of the activity and prevalence of flies which were obtained by actual counts. He also adduced bacteriological evidence, and it is stated that one fly was found to be carrying over one hundred thousand faecal bacteria.

Bacteriological evidence.—In addition to the evidence of Jackson, to which reference has been made, further proof that flies are able to carry the typhoid bacillus has been available for some years. Celli (1888) recovered the *Bacillus typhi abdominalis* from the dejections of flies which had been fed on cultures of the same, and he was able to prove that they passed through the alimentary tract in a virulent state by subsequent inoculation experiments. Ficker (1903) found that when flies were fed upon typhoid cultures they could contaminate objects upon which they rested. The typhoid bacilli were present in the head and on the wings and legs of the fly five days after feeding, and in the alimentary tract nine days after. Firth and Horrocks (1902), in their experiments, took a small dish containing a rich emulsion in sugar made from a twenty-four-hour agar slope of *Bacillus typhosus* recently obtained from an enteric stool and rubbed up with fine soil. This was introduced with some infected honey into a cage of flies together with sterile litmus agar plates and dishes containing sterile broth, which were placed at a short distance from the infected soil and honey. Flies were seen to settle on the infected matter and on the agar and broth. The agar plates and broth were removed after a few days, and after incubation at 37° C. for twenty-four hours colonies of *Bacillus typhosus* were found on the agar plates and the bacillus was recovered from the broth. In a further experiment the infected material was dusted over with fine earth to represent superficially buried dejecta, and the bacillus was isolated from agar plates upon which the flies had subsequently walked, as in the former experiment. They also found the bacillus on the heads, wings,

legs and bodies of flies which had been allowed to have access to infected material. Hamilton (1903) recovered *Bacillus typhosus* five times in eighteen experiments from flies caught in two undrained privies, on the fences of two yards, on the walls of two houses and in the room of an enteric fever patient. A series of careful experiments were made by Sellars<sup>1</sup> in connection with Niven's investigations on the relation of flies to infantile diarrhœa. Out of thirty-one batches of house-flies carefully collected in sterilised traps in several thickly populated districts in Manchester he found, as a result of cultural and inoculatory experiments, that bacteria having microscopical and cultural characters resembling those of the *Bacillus coli* group were present in four instances, but they did not belong to the same kind or variety. Buchanan (1907) was unable to recover the bacilli from flies taken from the enteric ward of the Glasgow Fever Hospital. Flies were allowed to walk over a film of typhoid stool and then transferred to the medium (Grünbaum and Hume's modification of MacConkey's medium), and subsequently allowed to walk over a second and a third film of medium. Few typhoid bacilli were recovered and none from the second and third films. Sangree (1899) performed somewhat similar experiments to those of Buchanan and recovered various bacilli in the tracks of the flies. This method of transferring the flies immediately from the infected material to the culture plate is not very satisfactory, as I have already pointed out (1908), as it would be necessary for the flies to be very peculiarly constructed not to carry the bacilli. The fly should be allowed some freedom before it has access to the medium to simulate natural conditions. Experiments of this kind were carried out in the summer of 1907 by Dr. M. B. Arnold (superintendent of the Manchester Fever Hospital) and myself. Flies were allowed to walk over a film of typhoid stool and then were transferred to a wire cage, where they remained for twenty-four hours with the opportunity

<sup>1</sup> Recorded in the 'Report on the Health of the City of Manchester, 1906,' by James Niven, pp. 86-96.

of cleaning themselves, after which they were allowed to walk over the films of media. Although we were unable to recover *B. typhosus* the presence of *B. coli* was demonstrated. *B. coli* was also obtained from flies obtained on a public tip upon which the contents of pail-closets had been emptied; the presence of *B. coli*, however, may not necessarily indicate recent contamination with human excrement. Aldridge (l. c.) isolated a bacillus apparently belonging to the paratyphoid group from flies caught in a barrack latrine in India during an outbreak of enteric fever. In appearance and behaviour to tests it was very similar to *B. typhosus*.

Although we are not certain yet as to the specific organism or organisms which cause the intestinal disease known as infantile or summer diarrhœa, which is so prevalent during the summer months and is responsible for so great a mortality among young children, I think we must consider the relationship of *M. domestica* and its ally *Homalomyia canicularis* to this disease epidemiologically similar to typhoid fever.

## 2. Anthrax.

In considering the relation of flies to anthrax several facts should be borne in mind. As early as the eighteenth century it was believed that anthrax might result from the bite of a fly, and the idea has been used by Murger in his romance 'Le Sabot Rouge.' A very complete historical account of this is given by Nuttall (1899). Most of the instances in support of this belief, however, that flies may carry the infection of anthrax, refer to biting flies. As I have already pointed out, *M. domestica* and such of its allies as *H. canicularis*, *C. erythrocephala*, *C. vomitoria*, and *Lucilia cæsar* are not biting or blood-sucking flies. The nearest allies of *M. domestica* which suck blood in England are *S. calcitrans*, *Hæmatobia stimulans* Meigen, and *Lyperosia irritans* L.; the rest of the blood-sucking flies which may be considered in this connection belong to the family *Tabanidæ*, including the common genera *Hæma-*

lopota, *Tabanus*, and *Chrysops*. These biting and blood-sucking flies live upon the blood of living rather than dead animals. But it is from the carcasses and skins of animals which have died of anthrax that infection is more likely to be obtained, and I believe that such flies as the blow-flies (*Calliphora* spp.), and sometimes *M. domestica* and *Lucilia cæsar*, which frequent flesh and the bodies of dead animals for the purpose of depositing their eggs and for the sake of the juices, are more likely to be concerned in the carriage of the anthrax bacillus and the causation of malignant pustule than are the blood-sucking flies. Consequently, as *M. domestica* and its allies only are under consideration, and for the sake of brevity, the relation to anthrax of the non-biting flies only will be considered here.

The earliest bacteriological evidence in support of this belief was published by Raimbert (1869). He experimentally proved that the house-fly and the meat-fly were able to carry the anthrax bacillus, which he found on their probosces and legs. In one experiment two meat-flies were placed from twelve to twenty-four hours in a bell-jar with a dish of dried anthrax blood. One guinea-pig was inoculated with a proboscis, two wings and four legs of a fly, and another with a wing and two legs. Both were dead at the end of sixty hours, anthrax bacilli being found in their blood, spleen, and heart. He concludes: "Les mouches qui se posent sur les cadavres des animaux morts du Charbon sur les dépouilles, et s'en nourrissent, ont la faculté de transporter les virus charbonneux déposé sur la peau peut en traverser les différentes couches." Davaine (1870) also carried out similar experiments with *C. vomitoria*, which was able to carry the anthrax bacillus. Bollinger (1874) found the bacilli in the alimentary tract of flies that he had caught on the carcass of a cow dead of anthrax. Buchanan (l. c.) placed *C. vomitoria* under a bell-jar with the carcass of a guinea-pig (deprived of skin and viscera) which had died of anthrax. He then transferred them to agar medium and a second agar capsule, both of which subsequently showed a profuse growth

of *B. anthracis* as one might expect. Specimens of *M. domestica* were also given access to the carcass of an ox which had died of anthrax; they all subsequently caused growths of the anthrax bacillus on agar. I entirely agree with Nuttall, who says: "It does seem high time, though, after nearly a century and a half of discussion, to see what would be the result of properly carried out experiments. That ordinary flies (*M. domestica* and the like) may carry about and deposit the bacillus of anthrax in their excrements, or cause infection through their soiled exterior coming in contact with wounded surfaces or food, may be accepted as proven in view of the experimental evidence already presented."

### 3. Cholera.

One of the first to suggest that flies may disseminate the cholera spirillum was Nicholas (1873), who, in an interesting and prophetic letter, said: "In 1849, on an occasion of going through the wards of the Malta Hospital, where a large amount of Asiatic cholera was under treatment, my first impression of the possibility of the transfer of the disease by flies was derived from the observation of the manner in which these voracious creatures, present in great numbers, and having equal access to the dejections and food of the patients, gorged themselves indiscriminately, and then disgorged themselves on the food and drinking utensils. In 1850 the 'Superb,' in common with the rest of the Mediterranean squadron, was at sea for nearly six months; during the greater part of the time she had cholera on board. On putting to sea the flies were in great force, but after a time the flies gradually disappeared and the epidemic slowly subsided. On going into Malta Harbour, but without communicating with the shore, the flies returned in greater force, and the cholera also with increased violence. After more cruising at sea the flies disappeared gradually, with the subsidence of the disease. In the cholera years of 1854 and 1866 in this country the periods of occurrence and disappear-



ance of the epidemics were coincident with the fly-season." Buchanan (1897), in a description of a gaol epidemic of cholera which occurred at Burdwan in June, 1896, states that swarms of flies occurred about the prison, outside which there were a number of huts containing cholera cases. Numbers of flies were blown from the sides where the huts lay into the prison enclosure, where they settled on the food of the prisoners. Only those prisoners who were fed in the gaol enclosure nearest the huts acquired cholera, the others remaining healthy.

Bacteriological evidence.—Maddox (1885) appears to have been the first to conduct experiments with a view to demonstrating the ability of flies to carry the cholera spirillum, or, as it was then called, the "comma-bacillus." He fed the flies *C. vomitoria* and *Eristalistenax* (the "drone-fly") on pure and impure cultures of the spirillum, and appears to have found the motile spirillum in the fæces of the flies. He concludes that these insects may act as disseminators of cholera. During a cholera epidemic Tizzoni and Cattani (1886) showed experimentally that flies were able to carry the "comma-bacillus" on their feet. They also obtained, in two out of three experiments, the spirillum from cultures made with flies from one of the cholera wards. Sawtchenko (1892) made a number of careful experiments. Flies were fed on bouillon culture of the cholera spirillum, and to be certain that the subsequent results should not be vitiated by the presence of the spirillum on the exterior of the flies, he disinfected them externally and then dissected out the alimentary canal, with which he made cultures. In the case of flies which had lived for forty-eight hours after feeding, the second and third cultures represented pure cultures of the cholera spirillum. Simmonds (1892) placed flies on a fresh cholera intestine, and afterwards confined them from five to forty-five minutes to a vessel in which they could fly about. Roll cultures were then made, and colonies of the cholera spirillum were obtained after forty-eight hours. Colonies were also obtained from a fly one and a half hours after having

access to a cholera intestine, and also from flies caught in a cholera post-mortem room. Uffelmann (1892) fed two flies on liquefied cultures of the cholera spirillum, and after keeping one of them for an hour in a glass he obtained 10,500 colonies from it by means of a roll culture; from the other, which was kept two hours under the glass, he obtained twenty-five colonies. In a further experiment he placed one of the two flies similarly infected with the spirillum in a glass of sterilised milk, which it was allowed to drink. The milk was then kept for sixteen hours at a temperature of 20–21° C., after which it was shaken, and cultures were made from it; one drop of milk yielded over one hundred colonies of the spirillum. The other fly was allowed to touch with its proboscis and feed upon a piece of juicy meat that was subsequently scraped. From one half of the surface twenty colonies, and from the other half one hundred colonies, of the spirillum were obtained. These experiments show the danger which may result if flies having access to a cholera patient, and bearing the spirillum, have access also to the food. Macrae (1894) records experiments in which boiled milk was exposed in different parts of the gaol at Gaya in India, where cholera and flies were prevalent. Not only did this milk become infected, but the milk placed in the cowsheds also became infected. The flies had access both to the cholera stools and to such food as rice and milk.

These foregoing experiments prove beyond doubt the ability of flies to carry the cholera spirillum, both internally and externally, in a virulent condition, and to infect food.

#### 4. Tuberculosis.

Although it may be considered to be hardly necessary to introduce flies as a means of disseminating the tubercle bacillus, it has, nevertheless, been proved experimentally that they are able to carry the bacillus in a virulent condition. As early as 1887 Spillman and Haushalter carried on experiments in which they found the tubercle bacillus in large

numbers in the intestines of flies from a hospital ward, and also in the dejections which occurred on the windows and walls of the ward. Hoffmann (1886) also found tubercle bacilli in the excreta of flies in the room where a patient had died of tuberculosis, and he also found the bacilli in the intestinal contents. One out of three guinea-pigs which were inoculated with the intestines died; two inoculations with the excreta had no effect, which led him to believe that the bacilli became less virulent in passing through the alimentary tract. But Celli (l. c.) records experiments in which two rabbits inoculated with the excreta of flies fed with tubercular sputum developed the disease. Hayward (1904) obtained tubercle bacilli in ten out of sixteen cultures made from flies which had been caught feeding on bottles containing tuberculous sputum. Tubercle bacilli were also recovered from cultures made from the fæces of flies which had fed in the same manner, which apparently caused a kind of diarrhœa in the flies, and they died from two to three days afterwards. Fæces of flies fed on tubercular sputum were rubbed up in sterile water and injected into the peritoneal cavity of guinea-pigs, which developed tuberculosis. Buchanan (l. c.) allowed flies to walk over a film of tubercular sputum and then over agar; a guinea-pig died of tuberculosis in thirty-six days by inoculating it with the resulting culture.

### 5. Ophthalmia.

Flies have been suggested as playing an important part in the spread of conjunctivitis, especially Egyptian ophthalmia, and although, so far as I have been able to discover, we have no bacteriological evidence in favour of the belief, the circumstantial evidence is sufficiently strong to warrant it.

In speaking of its occurrence at Biskra, Laveran (1880) says that in the hot season the eyelids of the indigenous children are covered with flies, to the attentions of which they submit; in this way the infectious discharge is carried on the legs and probosces of flies to the healthy children.

Dr. Andrew Balfour, of the Gordon College, Khartoum, in a letter to me, says that the Koch-Weeks bacillus is generally recognised as being the exciting cause of Egyptian ophthalmia. He says, "Ophthalmia is not nearly so common in the Sudan as in Egypt, nor are flies so numerous; doubtless the two facts are associated." Dr. MacCallan, of the Egyptian Department of Public Health, in answer to my inquiries, says that acute ophthalmias are more liable to transmission by flies than is trachoma. In his opinion the spread of the latter is, to a comparatively small extent, through the agency of flies, but it is mainly effected by direct contact of the fingers, clothes, etc.

The Koch-Weeks bacillus was first seen by Koch (1883) in Egypt in cases of acute catarrhal ophthalmia. He found that two distinct diseases were referred to under the name; in the severe purulent form he found diplococci, which he identified as very probably *Gonococci*; in the more catarrhal form he found small bacilli in the pus-corpuseles. He ascribed the propagation of the disease to flies, which were often seen covering the faces of children. Axenfeld (1908) states that "almost the only organisms occurring in acute epidemics of catarrhal conjunctivitis are the Koch-Weeks bacillus (perhaps also influenza bacillus), and the pneumococcus (in Egypt the gonococcus also, rarely *subtilis*). Other pathogenic conjunctival organisms<sup>1</sup> only exceptionally occur." And, further, "*Gonococci* and Koch-Weeks bacilli evidently lose their power of causing a conjunctivitis very slowly indeed, and are very independent of any disposition." His statement that, "on account of their great virulence and the marked susceptibility to them, a very small number suffices," is important in considering the relation of flies to the spread of the disease, although, as he remarks, every infection does not produce the disease. The fact that the Koch-Weeks bacillus cannot resist dryness cannot be urged as an argument

<sup>1</sup> In this connection he states (p. 236): "We can make the general statement that the staphylococcus in the conjunctiva is not contagious."

against the spread of the infection by flies, or the same would apply to the typhoid bacillus, whose carriage by flies is proven. Axenfeld mentions L. Müller and Lakah and Khouri as advocating the view that flies may spread the infection more readily. In view of the fact that, as the same author states, "Koch-Weeks conjunctivitis is to be classed with the most contagious infectious disease which we know of," it is important that the rôle of flies should be fully recognised. Notwithstanding the occurrence in this country of flies in less numbers than in such countries as Egypt, it would be well to bear in mind the probable influence of flies in cases of acute conjunctivitis, such as those described by Stephenson (1897) in our own country. The sole difference between the disease in Egypt and here is, as Dr. Bishop Harman points out to me in a letter, that "the symptoms produced (in Egypt) are, from climate and dirtiness of the subjects, more severe, and that there is found a greater number of cases of gonorrhœal disease than in England"; and, I would add, a far greater number of flies. This disease is eminently suited for dissemination by flies, both on account of the accessibility of the infectious matter in the form of a purulent discharge from the eyes and on account of the flies' habit of frequenting the eyes.

## 6. Plague.

Although fleas are considered to be the chief agents in the dissemination of the plague bacillus in spite of the fact that the proof is not absolutely convincing, it is nevertheless interesting, and certainly not unimportant, to refer to the series of experiments of Nuttall (1897) on *M. domestica*. In these experiments he conclusively proved that flies were able to carry the plague bacillus, and that they subsequently died of the disease. Flies were fed upon the crushed organs of animals which had died of plague. Control flies were fed in a similar manner on the organs of uninfected animals, and the control experiments were kept under the same conditions.

In two of the experiments the flies were all dead on the seventh and eighth days respectively, at a temperature of  $14^{\circ}$  C. At higher temperatures he found that flies died more rapidly. He was able to show that the flies contained the bacilli in a virulent condition for about two days after they had fed on infected organs; this, and the fact that the infected flies can live for several days, are extremely important from the practical standpoint, as indicating that flies should neither be allowed to have access to the bodies or excreta of cases of plague, nor to the food.

### 7. Miscellaneous.

There are on record a number of suggestions that flies may be responsible for the dissemination of other diseases caused by bacteria and other micro-organisms, and some account will now be given of these and the experiments in support of such beliefs.

If flies have access to wounds of an inflammatory and suppurative nature they are liable to transport the *Staphylococci* to other spots. Buchanan (1907) allowed *M. domestica* to walk over a film of *Staphylococcus pyogenes aureus* from an abscess, and afterwards over agar; a mixed growth resulted, in which *S. pyogenes aureus* predominated. Celli (l.c.) records experiments which proved that *S. pyogenes aureus* retains its virulence after passing through the intestine of the fly.

In the experiments carried out in 1907 by my friend Dr. M. B. Arnold and myself, he chose *B. prodigiosus* for the purposes of the experiment, as it is easily recognisable and not likely to be accidentally introduced. Flies which had just emerged from the pupæ, and therefore not already contaminated with an extensive bacterial flora, were allowed to walk over a film of the bacillus, after which they were confined to sterile glass tubes. At varying periods they were taken out and allowed to walk over the culture plates. Those confined for over twelve hours retained the bacilli on their



TABLE SHOWING SOURCES OF BACTERIA FROM FLIES.

Date.	Source.	Total number of bacteria.	Total acid bacteria.	Rapid liquefying bacteria.	Slow liquefying bacteria.	<i>Bacterium lactis acidii</i> , Group A, Class 1.	<i>Coli aerogenes</i> , Group A, Class 2.
1907							
July 27	(a) 1 fly, bacteriological laboratory	3,150	250	600	100	—	—
" 27	(b) 1 fly, bacteriological laboratory	550	100	—	—	—	—
Aug. 6	(c) 19 cow-stable flies	7,980,000	220,000	—	20,000	—	—
	Average per fly	420,000	11,600	—	1,000	—	—
" 14	(d) 94 swill-barrel flies	155,000,000	8,950,000	—	—	4,320,000	4,630,000
	Average per fly	1,660,000	95,300	—	—	46,000	49,300
" 14	(e) 144 pig-pen flies	133,000,000	2,110,000	100,000	266,000	933,000	1,176,000
	Average per fly	923,000	18,700	700	1,150	6,500	12,000
Sept. 4	(f) 18 swill-barrel flies	118,800,000	40,480,000	—	14,500,000	10,480,000	30,000,000
	Average per fly	6,600,000	2,182,000	—	804,000	582,000	1,600,000
" 21	(g) 30 dwelling-house flies	1,425,000	125,000	—	12,500	—	—
	Average per fly	47,500	4,167	—	417	—	—
" 21	(h) 26 dwelling-house flies	22,880,000	22,596,000	120,000	34,000	—	—
	Average per fly	880,000	869,000	4,600	1,300	—	—
" 27	(i) 110 dwelling-house flies	35,500,000	13,470,000	8,840,000	125,000	—	—
	Average per fly	322,000	124,200	80,300	1,100	—	—
Aug. 20	(j) 1 large blue-bottle blowfly	308,700	(a)	—	—	—	—
	Total average of 414 flies	1,222,570	367,300	7,830	73,500	—	—
	Average per cent. of 414 flies	—	30	6	6	—	—
	Average per fly of 256 flies, experiments (d), (e), and (f)	3,061,000	765,000	230	268,700	211,500	553,800
	Average per cent. of 256 flies, experiments (d), (e), and (f)	—	25	—	8	7	18

(a) 2200 mould spores.

appendages and transferred them subsequently to the culture media, but they were not recovered from those flies which were kept in confinement for twenty-four hours; a large number of flies, however, were not used.

Dr. Kerr, of Morocco, in a paper on "Some Prevalent Diseases in Morocco," read before the Glasgow Medico-Chirurgical Society (December 7th, 1906), described epidemics of Syphilis where, according to the author, the disease was spread by flies which had been feeding upon the open sores of a syphilitic patient.

Howard (1909) calls attention to an important investigation carried on by Esten and Mason (1908) on the rôle which flies play in the carriage of bacteria to milk. The flies were caught by means of a sterile net; they were then introduced into a sterile bottle and shaken up in a known quantity of sterilised water to wash the bacteria from their bodies and to simulate the number of organisms that would come from a fly falling into a quantity of milk. They summarised their results in the table given on p. 403.

From that table it will be seen that the numbers of bacteria carried by a single fly may range from 550 to 6,600,000, while the average number was about 1,222,000. Commenting on these results, the authors state that "early in the fly-season the numbers of bacteria on flies are comparatively large. The place where flies live also determines largely the numbers that they carry." From these results the importance of keeping flies away from milk and other food will readily be seen.

### VIII. FLIES AND INTESTINAL MYIASIS.

The larvæ of *M. domestica* and its allies are frequently the cause of intestinal myiasis and diarrhoea in children. The occurrence of the larvæ in the human alimentary tract may be accounted for in several ways. The flies may have deposited the eggs on the lips or in the nostrils of the patient, or the eggs may have been deposited on the food, subsequently

passing uninjured either as eggs or as young larvæ into the alimentary tract owing to insufficient mastication. Or the larvæ may have entered per rectum, the eggs having been deposited when the patient was visiting one of the old-style privies where these flies, especially *H. canicularis* and *H. scalaris*, frequently abound. These last two species are frequently the cause of this intestinal trouble, and it is most probable that the larvæ enter per rectum.

Owing to the inability on the part of the observers to distinguish the different species of dipterous larvæ we have little information as to their occurrence in these cases. Stephens (1905) records two cases. Two larvæ were procured which were stated to have been passed per rectum; one was *H. canicularis* and the other is described as *M. corvina*. The latter larva was stated to possess eight lobes on the anterior spiracular processes which "distinguishes these larvæ from *M. domestica*, which has seven only." I suspect this larva was *M. domestica*, which has six to eight lobes on the anterior spiracular processes. Some years ago a number of larvæ which had been passed by a child were sent to this laboratory, and I found that they were *M. domestica*. In 1905 some eggs taken from the stool of a patient suffering from diarrhœa were sent to me and on examination they proved to be the eggs of *C. erythrocephala*. The larvæ of the small house-fly, *H. canicularis*, as I have already mentioned, have occasionally been found in the stools of patients.

In certain cases the larvæ may wander from the mouth or alimentary tract and get into the nasal passages or other ducts, in which cases complications may ensue and result in the death of the patient.

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## X. APPENDIX.

### On the Breeding of *M. domestica* during the Winter Months.

In the account that I gave of the breeding habits of *M. domestica* in the second part of this monograph, it was stated (p. 503) that the experiments and observations pointed to the fact that, in the presence of suitable larval food, such as excremental matter or decaying and fermenting food materials in a moist and warm condition, the female flies would lay their eggs and the larvæ would develop if the temperature of the air was sufficiently high for the prolonged activity of the flies. Flies are sometimes found under these conditions in warm restaurants and kitchens, stables, and cowsheds, and under these conditions are able to breed during the winter months. I am pleased to find that my own observations and those of Griffith (there referred to) as to the ability of *M. domestica* to breed during the winter months has been confirmed by Jepson<sup>1</sup> during the past winter.

Flies were caught in February (1909) in the bakehouse of

<sup>1</sup> In “Reports to the Local Government Board on Public Health and Medical Subjects (New Series, No. 5). Preliminary Reports on Flies as Carriers of Infection. No. 3. Mr. Jepson’s Report on the Breeding of the Common House-Fly during the Winter Months,” pp. 5–8, 1909.

one of the colleges (Cambridge), and were transferred to a small experimental greenhouse in the laboratory where the temperature was from 65° F. in the morning to 75° F. in the evening. The flies were allowed to oviposit in moist bread in which the process of fermentation had begun. He found that the times for the developmental stages approximately agreed with those obtained by me at about the same temperature, and that the whole development was completed in about three weeks. At an average temperature of 70° F. the eggs were all hatched in twenty-four hours. The first larval stage lasted thirty-six hours, the second larval stage four days, and the third stage was complete in five and a half days; the whole larval period, therefore, occupied eleven days. The average period occupied in the pupal stage was ten days; some pupæ incubated at a temperature of 77° F. hatched in three days.

It may be stated now, therefore, without fear of contradiction, that flies are able to breed during the winter months, if the necessary conditions of food, temperature, and moisture are present. It is probably from these winter flies that the early summer flies are produced, as I have previously suggested.

#### CORRIGENDUM.

My attention has been very kindly called by Prof. W. A. Riley to a slight mistake that I have made in my account of the venation of the wing (Part I, p. 412). By an oversight I have termed transverse nervures the two small veins *m.cu.* (medio-cubital) and *cu.a.* (cubito-anal). These are really parts of the original longitudinal veins *M. 3* and *Cu. 2*. A study of such a series of dipterous wings as those figured by Comstock in the papers there quoted (Comstock and Needham, 1898), or in his 'Manual for the Study of Entomology,' will show that these apparent transverse or cross-veins are morphologically equivalent to branches of the primary veins.

THE UNIVERSITY;  
MANCHESTER.

## EXPLANATION OF PLATE 22,

Illustrating Dr. C. Gordon Hewitt's paper on "The Structure, Development, and Bionomics of the House-fly, *Musca domestica*, Linn. Part III. The Bionomics, Allies, Parasites, and the Relations of *M. domestica* to Human Disease."

Fig. 1.—Mature larva of *Homalomyia canicularis*, L.  $\times 17$ . *a.sp.* Anterior spiracular processes. *p.sp.* Posterior spiracular apertures.

Fig. 2.—Posterior end of mature larva of *Anthomyia radicum* Mg. *an.* Anus.

Fig. 3.—Anterior spiracular process of mature larva of *A. radicum*.

Fig. 4.—Head of *Stomoxys calcitrans*, L.; left lateral aspect.

Fig. 5.—Posterior end of mature larva of *S. calcitrans*.

Fig. 6.—Posterior spiracle of the same, enlarged.

Fig. 7.—Posterior spiracle of mature larva of *Musca domestica*.

Fig. 8.—Posterior spiracles of first larval stage of *Calliphora erythrocephala*, Mg.

Fig. 9.—Posterior spiracles of second larval stage of *C. erythrocephala*.

Fig. 10.—Posterior spiracle of mature larva of *C. erythrocephala*.

Fig. 11.—Anterior spiracular process of mature larva of *C. erythrocephala*.

Fig. 12.—Posterior end of mature larva of *C. erythrocephala*.

Fig. 13.—*Chernes nodosus*, Schr.  $\times 30$ .

Fig. 14.—Thoraco-abdominal region of *Homalomyia canicularis*, ♀, showing Gamasids attached to the ventral side of the abdomen.

Fig. 15.—Longitudinal (sagittal) section of abdomen of *M. domestica*, which has been killed by *Empusa muscæ*, showing the feltwork of fungal hyphæ filling the inside of the abdominal cavity and the production of conidia in the intersegmental regions.  $\times 12$ . *c.* Conidiophores producing conidia. *f.* Fungal hypha.

Fig. 16.—Four conidiophores showing the formation of conidia (*c.*)  $\times 100$  (approx.).

Fig. 17.—Conidium of *Empusa muscæ*.  $\times 400$ . *o.g.* Oil globule.

Fig. 18.—*Habronema muscæ* (Carter). Adult but immature specimen.  $\times 85$ . *g.a.* Genito-anal aperture.

Fig. 19.—Caudal end of *Habronema muscæ*.  $\times 360$ .

Fig. 20.—Tarsal joints of one of posterior pair of legs of *Musca domestica*. Lateral aspect, to show densely setaceous character.